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THE TERTIARY NON-MARINE MOLLUSCA OF SOUTH AMERICA

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By
Juan J. Parodiz
Curator of Invertebrates
Carnegie Museum

ANNALS OF CARNEGIE MUSEUM
PITTSBURGH, PA.
Vol. 40

THE TERTIARY NON-MARINE MOLLUSCA OF SOUTH AMERICA

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Abstract

The known species of continental mollusks from the South American Tertiary represent 22 families and 48 genera. Of the discussed species 37 per cent are from the Paleocene, 13 per cent the Eocene, 14 per cent the Oligocene, 24 per cent the Miocene and 19 per cent the Pliocene. In these percentages are included some species that occur in more than one epoch. Although the species of the Recent fauna are very similar to those of the Tertiary, the actual number of species that survived without substantial change amounts to only about 5 per cent. The oldest living species survives from the Oligocene: *Diplodon chilensis;* another four from the Miocene-Pliocene: *Diplodon guaranianus, Strophocheilus globosus* and *haemastomus,* and *Cyclodontina dentata;* and *Porphyrobaphe iostoma* and *Strophocheilus lutescens* from the Pliocene only. Two families, Viviparidae and Valvatidae, have been extinct in South America since the Paleocene, as have some genera of Pleuroceridae, Thiaridae, and Corbiculidae. But all the others, especially the Hyriidae, went through intensive adaptive radiation into modern forms. On the other hand, those that reached higher evolutionary stages in very early times modified little as groups of species but show extreme variability in populations and individuals of the Recent fauna, and adapted to different environments without genetic consequences.

The new taxa here described or named are mostly Paleocene: *Eriphyla miraflorensis, Lioplacodes feruglioi* and *bolivianus, Paleoanculosa* (new genus) *patagonica, Pyrgulifera sehuena* and *Potamides chaliana; Lymnaea klappenbachi* and *Taphius waltheri* from the Oligocene; *Neocorbicula stelzneri* from the Miocene; and *Epiphragmophora feruglioi* from the Pliocene.

The stratigraphic position and age of the species have been updated, correlated, and in many cases corrected. Many of the Paleocene forms were originally described as from the upper Cretaceous, since in the time-scale of earlier works the Danian was usually included in it. Paleocene-Eocene fossils are, in different and widely separated localities, of similar genera and are sometimes the same species. The conditions in which they lived were also similar: estuaries and fresh-water streams emptying into the sea, or strands of marshy, bay-like environments, in which the fresh-water species are found somewhat

mixed with the brackish-water or marine. The unstableness of the coast line is a characteristic feature of the Paleocene, and the correlation with marine formations is of great help in determining the relative age of the continental deposits.

The Paleocene fauna is mostly of North American origin. Some of the genera are known from the Cretaceous of Wyoming, and even the Triassic of Pennsylvania. A one-way migration of fresh-water mollusks occurred after the first communication between the Americas was established at the end of the Cretaceous. This migration was correlative with that of the early mammals which appeared for the first time in South America in the Rio Chico formation. The location of many of the early Tertiary fossils seems to indicate that the route of migration was along the west coast of present South America. A second, this time a two-way, migration occurred at the end of the Miocene and early Pliocene, with an exchange of taxa between South and Central-North America. The new taxa entering that newly formed Neotropical region were Ampullariidae, Aperostomidae, Streptaxidae and Xanthonycidae. And typical South American families, as Bulimulidae, penetrated North America as far north as Illinois. Our knowledge of the distribution of the fauna in Recent times indicates that such migrational changes continue today.

A small number of families, as Strophocheilidae, Chilinidae, and Bulimulidae are autochthonous to South America, and their oldest known fossils are Paleocene. *Epiphragmophora,* endemic in the Recent fauna, and with many species, is from a family of North American origin introduced in the Pliocene. Other endemic genera, as *Neocorbicula* and *Potamolithus,* belong to families of world-wide, past and present, distribution.

Paleozoic-Mesozoic genera of naiad-like mussels, such as *Naiadites, Carbonicola, Uniona, Kidokia,* and *Terraia,* were found in localities of the area considered as old Gondwana, but they are not relatives of the fresh-water mussels known from the Tertiary and Recent faunas. There is not positive evidence that any of the Tertiary-Recent non-marine mollusks of South America are directly related to the African fauna, and the examples given in early studies were cases of convergence (*Strophocheilus* and *Burtoa*) or simple errors of identification, as the "*Pleiodon*" *priscus,* which is actually one of the Hyriidae (*Paxyodon*).

Some families, as Lymnaeidae, Planorbidae, Physidae, are very poor in fossils and represent groups of world-wide distribution, whose original centers of dispersion are unknown.

The results of this study confirm, in general, Pilsbry's hypothesis elaborated in the first decade of this century. Added credit is due Pilsbry because very few fossils were known in his time, and he had to base his conclusions solely on his knowledge of the Recent fauna.

Introduction

This work is intended as the first comprehensive account of all the fresh-water and terrestrial mollusks known from the South American Tertiary. For students of this malacofauna, it has been difficult to cope with the paleontological data as a whole. The recognized and listed species or subspecies amount only to 137, a rather small number when compared with the innumerable marine species described for the same time and area, and yet this compilation represents a considerable, time-consuming task: the search for types, the very large bibliography including literature not always easily available, checking the accuracy of the references from old collections and geological papers, and the problems concerning taxonomy and the relative age of the fossils.

Taxonomic nomenclature has been updated as far as possible, in awareness that new discoveries and future systematic research would modify in part the present arrangement. Classification of Recent fresh-water mollusks is still far from satisfactory in many groups. Certain characters at the family-genus level offer evidences of convergence or parallelism, and without anatomical information at hand, the results may be confusing, which is precisely the case of fossils classified by conchological features alone. For the early authors, every minor variation constituted a taxonomic value. The concept of homoplasy was almost unconsidered. Some species, or even genera, have dual characteristics and, when anatomy is unknown, "classification" or identification was a matter of the student's choice.

Paleontological sequence or relationships were also obscured by early claims of an older age for many of the fossils, marshalling the evidences to answer the requirements of particular tendencies. Until late in the thirties concepts prevailed that complete faunas, now properly known of Paleocene age, were Cretaceous.

Very few new taxa, genera, or species have been introduced in this paper, and only when the material allowed for distinguishing clearly the differences added to the separation in time or space. The revision of the fauna also gave opportunity to evaluate the opinions on probable origin or centers of dispersion. This is discussed in the final chapters.

The earliest collections of fossil mollusks in South America were mainly made by d'Orbigny and Darwin, although these were mostly marine. Gabb and Conrad were the first to study the Pliocene fresh-

water fauna of Peru. During the last years of the 19th century and the beginning of the 20th, Hartt, Ihering, Mayer-Eymar, and White contributed to the knowledge of the oldest Tertiary species of Brazil and Argentina. Subsequently, Woods, Steinmann, Pilsbry & Olsson, Marshall, Palmer and others worked on materials from Peru northward to Colombia.

A great deal of work is still needed to clarify the stratigraphy of the Cretaceous-Tertiary boundary in large areas of Brazil. Argentine stratigraphy, especially of the Patagonian region, once very confusing, is now reasonably clear because of the contribution of many workers, especially the paleontologist G. G. Simpson and the geologist E. Feruglio. The considerable paleontological work of Ihering was primarily based on collections made by the brothers F. and C. Ameghino, and by Roth and Hauthal. Wichmann, Windhausen, and Frenguelli, added to the knowledge of the fossils and geology of Argentina and Uruguay.

ACKNOWLEDGMENTS

In expressing appreciation to the colleagues who contributed materials, information, or suggestions for this work, I wish first to honor the memory of those friends who are no more of this world: Dr. E. Feruglio of the Argentine Oil Bureau (Y.P.F.) who for 30 years explored Patagonia, accomplishing a monumental geological work; Dr. J. Frenguelli, former director of La Plata Museum; Dr. Noemi Cattoi, paleontologist of the Buenos Aires Museum, and its former director, Prof. M. Doello-Jurado.

I wish also to thank Dr. M. Birabén, present Director of the Buenos Aires Museum, its Curator of Invertebrates, Prof. Elena Martinez Fontes, and that museum's former Curator of Paleontology, Dr. A. Bordas; Dr. M. Klappenbach of the National Museum of Montevideo; Dr. A. A. Bonetto, Director of the Institute of Limnology, Santa Fe, Argentina; Dr. J. Stuardo of the University of Concepción, Chile; Dr. H. G. Richards of the Academy of Natural Sciences of Philadelphia for loan of type materials; Dr. J. P. E. Morrison of the United States National Museum for his suggestions regarding the taxonomy of "melanids"; Dr. K. v. R. Palmer of the Paleontological Institution, Ithaca, New York; Dr. C. P. Nuttall of the British Museum (Natural History); and Dr. A. Zilch of the Senckenberg Museum, Frankfurt, for information and photographic materials on nayades types.

TYPE-DEPOSITORIES

AMNH — American Museum of Natural History, New York
ANC — Academia Nacional de Ciencias, Córdoba, Argentina
ANSP — Academy of Natural Sciences of Philadelphia
BMNH — British Museum (Natural History)
CM — Carnegie Museum, Pittsburgh
IML — Instituto Miguel Lillo, Tucumán, Argentina
MACN — Museo Argentino de Ciencias Naturales, Buenos Aires
MLP — Museo de La Plata, Argentina
MNRJ — Museu Nacional do Rio de Janeiro
MP — Museu Paulista, São Paulo
NR — Naturhistoriska Riksmuseet, Stockholm
PRI — Paleontological Research Institution, Ithaca, New York
USNM — United States National Museum, Washington
ZIUZ — Zoologischen Institutes der Universität Zürich

Time Units and Correlations

The nomenclature and definition of the stages in stratigraphy are discussed in this paper in terms of time-units, to indicate the relative age of the fossil mollusks, without especial consideration of the physical or structural character of the rock-units. In the old literature of South American stratigraphy no clear distinction was made among rock-units, time-units, and faunistic types or cycles. All were included under single "formational" denominations, usually coined by adding the suffix "ense" to the name of the typical generic taxon of the stage. An example is the formation bearing the fauna with the fossil mammal *Notostylops* ("Notostylopense") which is now known as the Casamayor Formation of Casamayoran age. Subdivisions were named by adding the words "basal" or "cuspidal" in relation to their position to the main formational body.

Marine stages were usually better identified than continental, and fresh-water deposits were less clearly defined. Some marine complexes are here given what may seem lengthy discussion for a work dealing with non-marine invertebrates, but the relative sequence and correlation could not possibly have been drawn otherwise. Although lists of marine fossils to support such correlations are not included, these faunas were given adequate consideration during the research. Many of the marine Tertiary local faunas have been previously described and catalogued independently, and comparative studies of marine stages of the same age but from different regions are few. Thus we do not know certainly what relationship if any, would be revealed by a comparison between the Piraban marine fauna of Brazil with that of the almost coeval Paranan in Argentina. Considerable nomenclatorial duplication is to be expected. But when two marine stages follow a local sequence, the changes or similarities may be conspicuous and so evaluated in relation to age. On the other hand, certain marine faunas that previously had been considered as successive but separated, as the Rocanean and Salamancan, show elements of local facies but no time-units. In areas such as Uruguay, where early Tertiary marine stages are so poorly represented, the difficulty of establishing a correlative age for the fresh-water deposits increases.

PALEOCENE

The different fresh-water formations of early Tertiary age in South America are, structurally and faunistically, very similar. Non-marine fossils have frequently been found juxtaposed, or sometimes mixed, with underlying marine or brackish-water beds. These conditions correspond to those of estuary, bay, or strand of shallow sea areas. Ancient continental shores of the Paleocene, from Colombia to Patagonia, can be tentatively reconstructed because of such deposition where fresh-water bodies empty into the sea.

Even if all the formations cannot be correlated exactly, many of these deposits in Brazil, Peru, Chile, and southern Argentina show a malacofaunistic continuity from Danian to Thanetian, correlative with transgressions and regressions of the sea. Most marine beds of that age were once considered Cretaceous — before Danian became recognized as Paleocene — and consequently the terrestial and fresh-water chronological equivalents were misplaced in the sequence. This produced a long-lasting confusion and many paleontologists assumed that remains of dinosaurs were found in the same strata as early mammals and fresh-water mollusks. In certain places, it is possible that some of the correlated marine beds began to be deposited very early, so as to resemble a continuation from the Mastrichtian. That also accounts for the difficulties encountered by geologists in establishing the Cretaceous-Tertiary boundary.

The wide discrepancy which prevailed in the literature about the limit Senonian-Paleocene was not so much the result of wrong observations as the consequence of an obsolete time-scale applied by the early observers. No author before G. G. Simpson (1935b.) introduced the correct time correlation of the Paleocene in the Patagonian sequence. Previously, extreme points of view placed the early Tertiary strata now in the Senonian, then in the Eocene, with nothing in between. Windhausen was among the first to recognize (1918) that Salamancan was Danian. It was only when the Danian was escalated to lower Paleocene position that the problem began to clear. Ameghino was correct in placing the "Sehuennian" in the Danian, but not so with the "Capas de *Pyrotherium*" (= Deseadian) which is lower Oligocene. G. G. Simpson, who in earlier papers (1935b.) also had considered Salamancan as Senonian, finally gave further evidence of it as Paleocene (1940-1948).

BAHIA SERIES (*Northeastern Brazil*)

The first reference of mollusks from Bahia was made by S. Allport more than a century ago. Later (1870) Ch. Hartt described several fresh-water species, naming series of deposits the Bahia Group and placing it, with certain doubts, in the Neocomian. Ch. A. White (1887) made a revision of these fossils, adding new species (a total of 11 including a *Neritina*), and considered that small fauna peculiarly Cretaceous but containing types "represented among mollusks now living" (1887:233). On this account, Branner (1904) stated that these mollusks were of no use for establishing the age of Bahia.

According to Oliveira Roxo (1936) the lacustrine Bahia Beds were deposited in a tectonic depression of mid-Senonian age. The sedimentary complex of Bahia offers a varied structure from which several different formations have been indicated — Santo Amaro, Ilhas, São Sebastião (Martins 1959) — with the lacustrine deposits filling the eroded Senonian surfaces. Other coeval marine formations, such as Maria Farinha at Recife (north of Bahia) are now better identified as Paleocene. Penna (1965) studied the marine fauna of Maria Farinha, concluding that it was deposited in shallow waters of an unstable coast affected by epirogenetic movements. Such a condition is very similar to that of the San Jorge Sea of the same age and the Puca formation of Peru and Bolivia. In all probability Maria Farinha is chronologically equivalent to Roca-Salamanca. As to fossil contents, Bahia corresponds to early Paleocene, and Harrington (1956) also considered the correlated São Sebastião as Paleocene. Brackebusch (1883) anticipated this conclusion when comparing the Bahia Group of Hartt with the Salta System (Pucan) of northwestern Argentina.

With the exception of *Neritina*, which is peculiar to brackish-water flats, the other species from Bahia are fluvial or lacustrine:

?*Taphius monserratensis* (Hartt)
Lioplacodes lacerdae (Hartt)
Lioplacodes williamsi (Hartt)
Pachychilus terebriformis (Morris)
Pachychilus nicolayana (Hartt)
Neritina prolabiata (White)
Sphaerium ativum (White)
?*Anodontites totiumsanctorum* (Hartt)
?*Anodontites hartti* (White)
?*Anodontites mawsoni* (White)
?*Anodontites allporti* (White)

C. Maury (1934) described *Diplodon lucianoi* (also from northeastern Brazil, the Peixe River Series at Paraiba), considered Triassic, or Cretaceous by other authors. This species is not a *Diplodon* but rather some old genus of Cardiniidae *(Anoplophora ?).*

ITABORAIAN (*East-central Brazil*)

Several species of land snails from a limestone quarry a few miles northeast of Niterói, State of Rio de Janeiro, were described in 1935 by C. Maury. The complex of strata was originally indicated as upper Miocene or lower Pliocene. G. G. Simpson (1947) describing a new species of marsupial (*Eobrasilia*) from the same beds, correlated Itaborai with the Casamayor formation of Patagonia (lower Eocene). Paula Couto (1949, 1952) studied the mammal fauna, and on account of the primitiveness of some genera (*Ernestokokenia, Carodnia*), previously known from the Rio Chico formation, referred them to the Paleocene, as did Martins (1959). Among the gastropods however, only one of Maury's species, *Strophocheilus sanctijosephi,* bears resemblance to those of Rio Chico. But those of other genera, *Brasilennea, Itaboraia,* and *Bulimulus* are of middle-upper Tertiary, as suggested by the original indication (Itaborai II), and considered as such by Oliveira & Leonardos (1943).

BAURUAN (*Southeastern Brazil*)

Iridina (*Pleiodon*) *priscus* Ihering (1912), described from strata of Itaimbe, Taquaritinga, São Paulo, was at first unidentified but subsequently assigned by Oliveira & Leonardos (1943: 606) to the Bauru formation, as Senonian. Ihering emphasized the importance of this fossil as an African element in the Brazilian Cretaceous, but judging by the characteristics of its hinge the species belongs to the genus *Paxyodon.* The upper section of Bauru contains fossil turtles of the genus *Podocnemis,* first known from the Cretaceous of Arkansas and recently discovered in the upper Puca formation of northern Argentina (Paleocene). Thus late Bauru is probably of that age, although its base may be Mastrichtian (Note 1).

URUGUAY

Paleocene outcrops are apparently absent in the Uruguayan territory. Following the Cretaceous (Sandstones of Guichon, Mercedes, and Asencio-Palacio), the first well-known Tertiary deposits are Eocene-Oligocene (Queguay Limestone), with *Planorbis, Lymnaea,* and *Strophocheilus.* The fresh-water fossils may be earlier (older

Queguay) from lakes that filled the erosive basins of Asencio. There were no marine transgressions in Uruguay at that time and age correlations cannot with certainty be made with those of the southern areas.

PUCAN (*Northwestern Argentina, Bolivia, Peru*)

The name "Puca" means Red Beds in Quechua. Oliveira & Leonardos (1943) recognized, following Steinmann, two systems in the Pucan complex: a lower, Cretaceous, named by Moura and Wanderley the Divisor formation, and the upper, Puca *sensu stricto,* which is lower Tertiary. The complex probably extends into northwestern Brazil, in Acre territory, but the paleontological content here is unsufficiently known. During the Cretaceous-Tertiary transition a western marine transgression covered a great part of the present Andean area and reached as far south as Tucumán in Argentina. Such transgression is apparently synchronal with that of the San Jorge Sea in Patagonia. Upper Puca is constituted by the fluvial-lacustrine deposits contemporary with the last phase of that sea. The deposits outline the strand. (Note 2).

The "Formación Petrolifera" of Brackebush, the "Calcareo-Dolomítico" of Bonarelli, and the Miraflores Limestone in Bolivia all belong to the same complex. Bonarelli (1927) described 65 species from northwestern Argentina, with many new genera, as a Triassic marine fauna of his "Salta System." In such inflationary taxonomy, Cossmann recognized that at least twelve of the species are all one and the same, of the genus *Brachycerithium.* But some of the *Brachycerithium* are now certainly known as belonging to *Pyrgulifera,* well known from the Cretaceous of Wyoming and also found in the Paleocene of Patagonia. The other species are fresh-water, "melanids," and the fauna is presently recognized as Tertiary Puca. Bonarelli's unfinished manuscript was completed by Groeber who was unable, at first intention, to correct the work, but a decade later expressed his formal opinion that the "Formación Petrolifera" can be placed in the oldest Tertiary and chronologically parallel with (his) "Rio Grande formation" (Danian). Groeber, however, was inconsistent in his successive statements, often including the same complex in the Senonian.

The old Tertiary age for lacustrine-estuarine Puca is also supported by recent discoveries in vertebrate paleontology. Cattoi & Freiberg (1958) found the fresh-water turtle *Podocnemis* in the Santa Barbara section of Puca in the province of Jujuy, northwest Argentina. The

migration of *Podocnemis* into South America probably took place at the same time as that of the early mammals and the fresh-water mollusks. Bonarelli's view of a Triassic age for the "Salta System" was still maintained by O. Haas (1953) but the fresh-water fauna, as well as the geological correlations made by Frenguelli (1937), Ahlfeld (1946), Schlagintweit (1941), and also Groeber, left no doubts of the Paleocene age of the Upper Puca (Note 3).

From the study of the fossils, Fritszche (1924), concluded that Puca was deposited in a marginal shallow basin, sometimes communicating with the sea, or closed and receiving fresh-water tributaries. More specifically, Frenguelli (1937) indicated a series of lacustrine basins which at some periods became united, the process being repeated with the variations of the water level. The marginal area formed reefs of calcareous algae, a good habitat for gastropods and poor for bivalves. These were conditions similar to those indicated by Groeber for Jahuel.

The recognized species from fresh-water Puca are (for Bonarelli's list of species see Appendix II):

Pachychilus bicarinata (Fritzsche) Peru
Neocorbicula dormitator (Pilsbry) Bolivia
Neocorbicula miraflorensis, new name, Bolivia
Sphaerium sp. Bolivia
Lioplacodes bolivianus, new name, Bolivia
Valvata yaviana (Fritzsche) Bolivia and N.W. Argentina
Valvata satira (Fritzsche) Bolivia and N.W. Argentina
Potamides potosensis (d'Orbigny) Bolivia and N.W. Argentina
Doryssa andicola (Pilsbry) Bolivia and N.W. Argentina
Taphius boliviensis (Fritzsche) Bolivia and N.W. Argentina
Doryssa maimarensis (Bonarelli) N.W. Argentina
Potamides turgidus (Bonarelli) N.W. Argentina
Potamides doelloi (Bonarelli) N.W. Argentina
Potamides decarlesi (Bonarelli) N.W. Argentina
Pyrgulifera feruglioi (Bonarelli) N.W. Argentina
Aylacostoma striata (Bonarelli) N.W. Argentina
Aylacostoma brackebuschi (Bonarelli) N.W. Argentina

LONQUIMAY AND LOWER CONCEPCION (*Central Chile*)

On the western slope of Sierra Pedregoso, at the Lonquimay Pass, upper Bío-Bío Valley, west of Arauco, Burckhardt (1900) found bitu-

minous shales of lacustrine origin containing a small fauna of mollusks described by Mayer-Eymar. The age was at that time identified as lower Eocene.

Northeast of Bío-Bío, in the zone of Concepción, new findings of fresh-water fossils mixed with brackish-water fossils (*Mytilus ramosus*) indicate an extension of the deposits between the two marine ones, Concepción formation above (also called Pre-Navidad) and the strata of Boca-Levu below (see Guiñazu 1940). The lower marine strata are chronologically, although not faunistically, equivalent to San Jorge (Roca and Salamanca), and so the fresh-water shells appear as a faunistic continuation of the Jahuel formation (part of Groeber Rio Grande formation; Note 4). The uppermost section of Concepción is considered Eocene, and Boca-Levu Paleocene or lowest Eocene, rather younger than Jahuel.

Frenguelli (1940) and Feruglio (1949) found the same fresh-water Fauna on the eastern side of the Andes in Patagonia (Neuquén, Chubut and Santa Cruz). The fossils of the upper Paleocene (Thanetian) Lonquimay, are (original generic designation in brackets):

Chilina fischeri (Mayer-Eymar) [*Actaeocina*]
Ancylus humboldti (Mayer-Eymar)
Potamolithus capitatus (Mayer-Eymar) [*Bythinia*]
Diplodon burckhardti (Mayer-Eymar) [*Unio*]

From Lower Concepción (upper Paleocene or lower Eocene):

Paleoanculosa araucana (Phillipi) [*"Paludina"*]
Potamolithus capitatus
Neocorbicula sp.

SANJORGIAN *(Southern Patagonia)*

Discussion of these marine beds is included here to clarify the correlation with fresh-water (Jahuel, Sehuen) and terrestrial strata (Rio Chico) of Rio Negro, Chubut, and Santa Cruz.

Wilckens (1905) named the marine complex of Roca and Salamanca "San Jorge-Stufe". Windhausen (1918) used the term in a restricted sense in studying the problem of the Cretaceous-Tertiary boundary, and defined the position of San Jorge, separating it from the marine Senonian (beds with *Lahillia luisa*; see Note 36). The two San Jorge facies, however, continued to be called by other authors Roca and Salamanca (Note 5).

The differences found between Roca and Salamanca are structural. The first is composed of argillaceous limestone, the second argillaceous sandstone (see Note 5). But the faunistic differences are minor and represent only zoogeographical sectors of deposition in the same way in which, at the present time, the molluscan fauna of San Matias Gulf (southern limit of the Argentine malacological province) differs from that of San Jorge Gulf (northern part of the Magellan province). And as it does today, the overlapping zone shared a number of common species in times past.

The northern facies, Roca, reaching as far west as Mendoza and La Pampa, was separated from the southern, Salamanca, by the quartz-porphyritc plateau of central Patagonia (Windhausen's Deseado Island), and another separation, but of lesser importance, took place between the northern and southern marine sedimentation in Santa Cruz (Note 6).

Sanjorgian sedimentation began earlier than Riochican, transgressively over the Chubutian (Senonian). During its regression shallow eroded areas remained, filled with Jahuel facies (Sehuen) in the south and Rio Chico in the north. The swampy, bay-like coastal line of the San Jorge Sea can be traced at the places where the marine and fluvial deposits mix.

The name "Rocaneen" was introduced by Ihering in 1903 (although these marine beds were recognized first by Doering in 1882), and its type locality is the plateau north of the village of General Roca in Rio Negro. Ameghino correlated it with his Sehuenian of Danian age. The term Salamancan was also introduced by Ihering on the same occasion (originally "Salamancaneen"; Ameghino's "Salamanqueen"), for similar strata of the coast of the San Jorge Gulf, north of Pico Salamanca (type locality, Punta Peligros).

Weaver (1927) thought that part of the Roca beds were also included in the Campanian-Mastrichtian, and this was also the idea of many authors before G. G. Simpson. Apart from age considerations, Weaver's observations were correct inasmuch as he indicated that the Roca transgression originated from southeast to northwest; "At the opening of the Roca epoch much of the above indicated appears to have been low lying and swampy, but as the marine waters advanced inland there was an oscillation of the shore-line, resulting in deposition of *alternating beds of freshwater, brackish and marine origin*" (Emphasis mine. J.J.P.).

G. G. Simpson first considered (1932) Salamancan as Cretaceous,

but soon (1933:11) established the correct correlations: "Rio Chico Formation overlies the Salamanca, or its lateral equivalent, with or without the interposition of a post-Salamanca terrestrial series. [footnote:] The Salamanca itself grades vertically and laterally into beds of essentially fresh-water character, and it is by no means clear that the beds properly included under this name are all marine)." This evidently refers to strata which are Jahuelian, or Sehuenian. The reason Simpson did not mention Roca was because the strata of northwestern Rio Negro were situated beyond his immediate area of research, but his important conclusion was that the Rio Chico fauna of mammals (Ameghino's "Notostylopense Basal") was not Cretaceous but Tertiary: between the middle Paleocene and lower Eocene, "upper Paleocene seems most likely" (1935b:20), and "Salamanca is older than Rio Chico but probably grades into the latter [and] there is considerable likelihood that Salamanca is really earliest Tertiary (early Montian or in the North American sequence Puercan) or perhaps transitional Danian Montian" (1941). As early as 1916, Windhausen also indicated that "The Roca horizon corresponds probably to the lowest part of Tertiary."

SEHUENAN (*Central and southern Patagonia*)

The term "Sehuense" or "Sehuenense" introduced by Ameghino in 1897-98 was for strata included in the "Red Sandstones" or "Guaranitic formation" of Senonian age, a heterogeneous complex of members such as: Salamancan, Rocan, *Lahillia Luisa* beds, (Cazadoran), all marine, the "Notostylops formation" (= Casamayor), the "strata with dinosaurs." The name derived from the locality of Sehuen-Aike on the Sehuen River (also called Chalia) of southern Santa Cruz. Its fauna is still poorly known: fresh-brackish-water gastropods, *Potamides*, a bivalve first described as *Astarte*, later transferred to *Corbula* and *Eryphilla;* from similar northern strata of the big bend of the Senguerr River, *Diplodon colhuapiensis;* and a small oyster, *O. guaranitica* (Note 7). In 1901-2 Ameghino placed the Sehuenan at the top of the following complex:

Sehuense – Upper, with *O. guaranitica*
Lower, with *Ostrea, Melania* and *Potamides*
Pyrotheriense (= Deseado)
Astraponotense (= Musters)
Notostylops Superior (= Casamayor)

Notostylops Inferior (= Rio Chico)
Pehuenche (Strata with dinosaurs)

If such sequence were acceptable within the ages today indicated for these stages, the Sehuenan would be placed in the Oligocene. But late in 1902, the same author restricted Sehuen to the lower section, which he began to call "Camaronense" (for Puerto Camarones). When in 1903 Ihering replaced the "marine equivalent of *Pyrotherium*" with the name "Salamanqueen," he maintained Sehuen as a southern occurrence of it. Reaching this point it was difficult indeed to identify the Sehuenan, and Wilckens (1905) reacted to such confusion by reducing the whole complex to two groups:

Above: "San Jorgestufe" = Roca + Salamanca + "Luisaschichten" (see Note 36).
Below: "Guaranitische Sandsteine" (with dinosaurs, mammals and fresh-water mollusks) corresponding to Ameghino-Doering's Pehuenche (see Note 35).

Rejecting again the apparent simplicity of Wilckens' dichotomy, Ameghino, in accordance with Ihering, produced his last classification (1906):

Pyrotheriense (now Deseado, Oligocene)
Sehuenense (less Camarones; now Paleocene)
Astraponotense (now Musters, Upper Eocene)
Notostylops Superior-Medio (now Casamayor, lower Eocene)
Notostylopense Basal (Salamanca included) (now Rio Chico, Paleocene)
Pehuenche Superior (now Roca-Salamanca, Paleocene)
Pehuenche Inferior (Cretaceous)

Geologists and paleontologists compromised on this scheme for many years, ignoring fresh-water fauna. Neither Windhausen (1918-Note 8), nor Wichmann (1918-1927), the only two authors who at that time made observations on lacustrine or brackish-water deposits, considered the correlations with Sehuen and it continued to be regarded as something entirely isolated in Santa Cruz. The neglect is more impressive inasmuch as *Diplodon colhuapiensis* was of considerable stratigraphic importance. The subject was extensively discussed by Frenguelli (1930a.), who placed the lower Sehuenan as equal to Wilckens' Sanjorgian, Keidel's "Daniense," and Ihering's Salamanca.

Frenguelli also questioned the advisability of applying the same nomenclature for equivalent series of northern and southern Patagonia. For the lower, and better known, marine formation he reserved "Salamanquense," using a more natural sequence for the southern Sehuen (The Chalia or Sehuen River, 500 miles away from Salamanca, is separated from the latter by the porphyritic plateau), as equivalent of Upper Jahuel (between Salamanca and Roca). Twenty years later the same author enlarged the concept of the Sehuenan, describing (Note 9) a corresponding fossil flora from Mata Amarilla. This was also described by Berry during the period 1925-1937. The plants were collected at the foot of a cliff south of Cerro Bagual, together with mollusks, *Potamides,* and *Eryphylla.* It was observed that the strata became thinner to the east and finally disappeared. If they had been only marine, as Feruglio (1935-1949) maintained, the process should have been inverse (Note 10). At Chalia River, as well as in the San Jorge zone, the Sehuenan is followed by tuffs which in Chubut are recognized as Riochican (Note 11).

Occurrence of Sehuen beds at Rio Senguer in Chubut, indicated by Ameghino, was verified by Ihering (1903) with the description of *Diplodon* from Colhue Huapi. The stage can be identified in this area with those strata often referred to as "Banco negro" within the Paleocene complex (relatively lower than Rio Chico: level "H" of G. G. Simpson's 1935b diagrammatic section of Cerro Redondo). At Rio Senguerr the same Banco Negro was indicated by Feruglio (1927) as on top of "Banco Verde" (with fishes), having Salamanca at the base. In 1949 (I:101,228) the same author mentioned it again as lying over the Riochican (Note 12).

The Sehuenan is in relation to the Riochican of the same alternate sequence indicated by G. G. Simpson (1941) for Salamancan: "older than Rio Chico but probably grades into the latter." According to Feruglio, the "Banco Negro" is a guide to establishing the transition between Salamanca and Rio Chico (1949, II:25) because of its color, singular constancy, and representation of marshy deposits with crocodiles, turtles, and fresh-water mollusks (Note 13).

These conditions change towards the north and northwest (Rio Negro and south of Mendoza), where separation between marine and fresh-water strata are sometimes more conspicuous (Roca overlies Jahuel). The Sehuenan, however, must have occurred occasionally there in view of the beds with *Paleoanculosa macrochilinoides* (Doello-Jurado). In the South (Santa Cruz) the impoverished fresh-

water fauna of the Paleocene represents late arrivals at the time when the San Jorge sea was in regressive phase, while the northern branch of the same sea (Roca) lasted perhaps as long as Rio Chico.

The Sehuenan is here recognized as a southern facies of the Jahuel formation, lateral equivalent of Rio Chico but smaller in development, embedded in the marginal areas of San Jorge (Note 14). The species of *Pyrgulifera* from Mata Amarilla confirms its fresh-water condition (Note 15). Feruglio also mentioned (1949:274) a *Nerinea,* but I did not find specimens of this genus when revising the materials collected by him.

JAHUELAN

The name "Capas de Jahuel" was introduced by Windhausen in 1914, who also made brief references to them in 1918 and 1924. The type locality, Jahuel or Jagüel, is near the eastern slope of Sierra Auca Mahuida and Bajo del Palo, south of Colorado River in Neuquén, but the greater development of the formation appears in Rio Negro. What originally was indicated as "lower Roca" with *Perna* and *Ostrea,* corresponding to what Wichmann (1927) called "lacustrine Senonian," contains all the Paleocene fresh-water beds of Patagonia, including the Sehuenan facies. After Windhausen, the only author who made reference to Jahuel as a distinct stratigraphic unit was Frenguelli (1930a.:32): "Jahuelense = Windhausen's lower Roca plus #2 level in Wichmann 1927," (and divided into an upper (= Sehuen) and lower (= Salamanca) Jahuel). We have already seen that by mechanics of deposition the fresh-water strata sometimes underlie Roca or Salamanca, and sometimes are parallel even with the Riochican.

At Rio Negro, whence most of the fossils have been described, Jahuel is found at several localities: General Roca, Bajo Menuco, Lenza Niyeu, Bajo Santa Rosa, Nahuel Niyeu. It also extends into Mendoza, (Cañadón Molles), San Luis (Alto Pencoso), and Neuquén (Ranquil, Chañar Grande, Contralmirante Cordero). Chronologically it is correlated to the Puca formation of Bolivia and Peru, but is closer to the Lonquimayan in Chile. Its terrestrial equivalent on the east is the Riochican.

The fossils known from Jahuel (some of which are abundant in specimens) are:

Diplodon colhuapiensis Ihering (Sehuen)
Diplodon bondenbenderi Doello-Jurado

Diplodon pehuenchensis Doello-Jurado
Neocorbicula dinosauriorum (Doello-Jurado)
Neocorbicula pehuenchensis (Doello-Jurado)
Neocorbicula sehuena (Ihering) (Sehuen)
Potamolithus windhauseni (Parodiz)
Potamides patagonensis (Ihering) (Sehuen)
Potamides chaliana Parodiz (Sehuen)
Pyrgulifera sehuena Parodiz (Sehuen)
Paleoanculosa patagonica Parodiz
Paleoanculosa bullia (Ihering)
Paleoanculosa macrochilinoides (Doello-Jurado)
Physa doeringi Doello-Jurado
Physa wichmanni Parodiz
Chubutolites sp. Ihering (Note 58)

RIOCHICAN

G. G. Simpson (1933:11) named Rio Chico formation the formerly upper Chubutian containing the oldest mammal fauna of Patagonia, which in Ameghino's nomenclature was known as "*Notostylopense* Basal." The same formation has been also called "Pehuenche," but Simpson rectified this mistake since the typical Pehuenche of Doering (1882) is Cretaceous, bearing the "Strata with dinosaurs," and no mammals occur in it (Note 17).

The Riochican is composed of sandstone and clay complexes, separated from the upper mammal bearing tuffs (Casamayor, Musters) of the Eocene. The history of the discovery and exploration of these beds has been fully discussed by G. G. Simpson (1941,1948), and need not be reviewed here.

The Riochican overlies the Salamancan, and its base is laterally equivalent to Sehuenan. As to paleontological contents, it is also equivalent to the Paleocene beds of Brazil at Itaborai. Being essentially terrestrial, fossil mollusks are rather scarce, but in 1931 Simpson collected casts of large land gastropods at Cañadon Hondo (which I described in 1946 as *Thaumastus*), a major locality for Riochican fauna but where also is found "an unusual variety of Casamayoran facies" (G. G. Simpson 1948:28). At this locality, or vicinity, Hauthal found fossil *Strophocheilus* of a single species older than the more abundant species of the Eocene tuffs. Inasmuch the families Bulimulidae and Strophocheilidae seem to be autochthonous to South America

(the oldest fossils are from Patagonia) the discovery of other species in the Riochican or Casamayoran is to be expected.

The fresh-water bed equivalent and coeval with Rio Chico is the Jahuelan.

EOCENE

Continental mollusks of Eocene age in South America are known in small number, from Colombia to Peru (fresh-water) and in Patagonia (mostly terrestrials). Those of the northwest appear mixed with marine, deposited under the same conditions that prevailed in Chile and Patagonia during the Paleocene, in fringe areas of regressive seas. But on the Atlantic side, a reversed situation accumulated thick terrestrial sediments, and in some areas, as in Uruguay, Eocene strata are entirely unknown and there is a large hiatus between the Upper Cretaceous and the Oligocene.

EOCENE CORRELATIONS

	COLOMBIA	PERU	CHILE	PATAGONIA
	Corrosan	Lobitosan		
		Saman		Mustersan
EOCENE	Toronan		Concepción	
	Lisaman	Upper Negritos		Casamayoran
PALEOCENE	Umir ?		Lonquimayan	Riochican

CORROSAN (*Los Corros formation, Colombia*)

This formation contains the oldest fresh-water tertiary mollusks of the northwestern section of the continent, well distinguished from the next, Mugrosan (Oligocene) fauna. It rests in unconformity over the Lisaman beds. Its age is considered upper Eocene (Bartonian?), and the few fossils belong, in part, to peculiar genera, from strata along the Sogamoso River and tributaries, betwen the Magdalena River and the western Andean slope of the oriental cordillera, in the province of Santander. Fossils known are:

Sogamosa cyrenoides Pilsbry & Olsson
Potamides mcgilli Pilsbry & Olsson
Doryssa corrosensis Pilsbry & Olsson
Diplocyma wheeleri Pilsbry & Olsson
Diplocyma succionis Pilsbry & Olsson

LOBITOSAN (*Lobitos formation, Peru*)

This is essentially a marine formation subdivided into faunistic series with *Turritella* and *Clavilithes*. The upper, Clavilithes series, rendered a single species of *Potamides* (*P. occidentalis* Wood). Whether *Pseudoglauconia* from the same series is truly fresh-water or a brackish-water form is still open to question.

CASAMAYORAN AND MUSTERSAN (*Patagonia*)

These two terrestrial formations were originally called by Ameghino, "Notostylopense" (Casamayor) and "Astraponotense" (Musters) considering the typical mammal genera they contain, and both integrating the whole Eocene in uplifting Patagonia. Also they correspond to the lower half of what Feruglio and other geologists used to call the "Sarmiento Group" or "Tobas [tuffs] con mamíferos" (Note 34), mainly formed by volcanic ashes uniformly spread. Known mollusks are:

Strophocheilus chubutiensis Ihering
Strophocheilus hauthali Ihering
Paleobulimulus eocenicus Parodiz
Chilina stenostylops Parodiz

The type locality of Casamayor is on the southern coast of the San Jorge Gulf, north of Mazaredo.

OLIGOCENE

Fresh-water mollusks of this epoch are known mainly from Colombia, La Cira, and Mugrosa formations, which may be correlated with the Zorritos formation of Peru with abundance of *Aylacostoma,* of which Pilsbry named at least ten species. The younger Laciran limits the Miocene at the top of the Colorado series of the Sogamoso River, but Laciran fauna is more diversified than that of Mugrosan.

In other continental areas the predominant mollusks known from the Oligocene are marine, with occasional fresh-water occurrences at distant places: Zorritos formation in Peru, Queguay limestone in Uruguay, and in the Cóndor River beds (Punta Arenas) on the Strait of Magellan. The age of the last deposits has not been established with certitude, but several authors have referred them to the Oligocene. Perhaps they correspond to strata similar to the "Terciario carbonífero" in Neuquén, containing plants *(Notophagus)* and fresh-water mussels *(Diplodon)* as a continental equivalent of the Magellanian beds.

QUEGUAY LIMESTONE *(Uruguay)*

Overlying the eroded surface of the upper Cretaceous Asencio sand-

stone (= Palacio) is the oldest Tertiary known in Uruguay, the Queguay limestone, rich with infiltrations of silica deposited in lacustrine environments of the southwest portion of the territory (Paysandú, Río Negro, Soriano, Flores, and Canelones), and typically represented in the Queguay valley, a few miles north of Paysandú. Because of the low deposition of the Tertiary lakes, these strata are sometimes found at a lower level than the Cretaceous sandstones, and the age of the strata formerly was indicated as probably Cretaceous. But the profile studied by Caorsi & Goñi (1958) at Soriano (Arroyo del Aguila) show the natural sequence from the base up: Asencio (Senonian), Queguay (Oligocene), Fray Bentos (Miocene) (Note 46).

RED BEDS OF PACHITEA RIVER *(Peru)*

Pilsbry considered the fossil fauna of the Pachitea River, with Ampullariidae, Thiaridae and Corbiculidae, to be synchronous with La Cira of Colombia, that is, upper Oligocene, although it is probable that the fauna is rather younger, on the Oligocene-Miocene boundary or lowest Miocene. In these beds the nayades, which are characteristic of La Cira, are lacking.

LACIRAN AND MUGROSAN *(Colombia)*

These formations are localized in the western side of the Magdalena valley, between the central and eastern cordilleras. Mugrosan is older (lower to mid-Oligocene), with greater development of *Aylacostoma.* Laciran, although richer in number of species, occurs sparsely between the Sogamoso and Oponcito rivers and contains typical fresh-water genera, *Aylacostoma, Doryssa, Pachychilus, Diplodon,* and *Lyrodes,* sometimes mixed with marine or low-salinity bivalves such as *Corbula* and *Mytilopsis.* As the Laciran fauna is rather modern in aspect, its age cannot be older than upper Oligocene. Above it lies the Real series of the Miocene, carrying silicified and carbonized fossil trunks and leaves, but barren of mollusks.

STRATIGRAPHIC LOCATIONS

	PERU	COLOMBIA	URUGUAY	PATAGONIA AND TIERRA DEL FUEGO
	Pachitea	La Cira	Queguay and Miguez limestone	"Minas de Carbón" (Río Cóndor)
OLIGOCENE	Upper Zorritos	Colorado		
	Low clay shales	Mugrosa		Magellanian beds
EOCENE	Lobitos	Los Corros	Ascencio	Musters

FRESH-WATER MOLLUSKS FROM THE OLIGOCENE

Colombia

Doryssa corrosensis (Pilsbry & Olsson)
Pachychilus gracillimus (Pilsbry & Olsson)
Aylacostoma paleus (Pilsbry)
Aylacostoma sigmachylus (Pilsbry & Olsson)
Aylacostoma mugrosana (Pilsbry & Olsson)
Aylacostoma eucosmica (Pilsbry & Olsson)
Aylacostoma waringi (Pilsbry & Olsson)
Aylacostoma laevicarina (Pilsbry & Olsson)
Pyrgulifera avus (Pilsbry & Olsson)
Lyrodes lacirianus (Pilsbry & Olsson)
Diplodon oponcitonis (Pilsbry & Olsson)
Diplodon latouri (Pilsbry & Olsson)
Anodontites lacirianus (Pilsbry & Olsson)

Peru

Ampullaria manco (Pilsbry)
Aylacostoma pictus (Pilsbry)
Potamides ornei infraliratus (Pilsbry)
Neocorbicula sp.

Uruguay

Taphius walteri Parodiz
Lymnaea klappenbachi Parodiz
Strophocheilus charruanus (Frenguelli)

Patagonia

Diplodon chilensis patagonicus (d'Orbigny)

Tierra Del Fuego

Diplodon nordenskjoldi (Steinmann & Wilckens)

Magallanes (Chile)

Neocorbicula chilensis (Soot-Ryen)

MIOCENE

The better known fresh-water fauna of the Miocene is that studied by Palmer (1941) from the Biblian-Cuencan-Azoguean series of Ecuador, and land shells of some species still living, from Uruguay. Several

Potamides have been described from Colombia, and other isolated species from Venezuela and Brazil.

REAL SERIES *(Colombia)*

Although the Colombian Miocene is characterized by fossil flora and often regarded as barren of mollusks (Wheeler 1935), there are *Potamides* indicated for the Real series (Note 46).

MONAGAS *(Venezuela)*

This series, from which the only fossil known is *Castalioides laddi* Marshall (= *Diplodon guaranianus biblianus*), is probably of mid-lower Miocene, equivalent to the following:

BIBLIAN-CUENCA-AZOGUES SERIES *(Ecuador)*

The deposits are known from a 25-mile strip along the Azogues River, from the Biblian in the north to the Paccha River in the south, in the southwestern section of Ecuador, Guayaquil Gulf zone (50 miles inland). The oldest series, the Biblian sandstone, contains *Shepardiconcha* (= *Doryssa*), *Diplodon, Anodontites,* and *Monocondylaea.* The middle Miocene is represented by the Cuenca shales overlying the Biblian, but also appears parallel to the Andesite, with genera allied to the southern *Potamolithus* and *Neocorbicula.* The upper section, Azogues sandstone, is not as thick as Cuenca but is more extensive in deposition, also containing *Neocorbicula* and the brackish-water *Neritina.*

FRAYBENTOSAN = "PALMIRENSE" *(Uruguay)*

The name Fray Bentos formation was proposed by Lambert (1939) for the loessoid silts which in a less defined sense had been called "Tosca terciaria," "Punta Gorda loess," "Palmirense" (Note 18), "infra," or "pre-Pampeano." The deposits in southwest Uruguay (Colonia, Punta Gorda, Palmira, for example,) are primarily aeolic in origin. The mollusks they contain consist of a few land snails, of species very close to or sometimes the same as those now living in the area or nearby *(Strophocheilus, Cyclodontina).* The upper part of Fray Bentos is of

MAP 1

1-19. Areas of Eogene deposits bearing continental molluscan fauna. 1-11. Paleocene. 12-14. Eocene. 15-19. Oligocene. 1. Bahia Series (1ª coeval Maria Farinha). 2. Itaboraian. 3. Bauruan. 4, 5. Pucan (Miraflores and "Calcareo-Dolomítico"). 6. Lonquimay and Bío-Bío. 7, 8. San Jorgean (northern Roca, southern Salamanca). 9. Riochican. 10. Sehuenian. 11, 11ª. Jahuelian. 12. Los Corros. 13. Lobitos. 14. Casamayor and Musters. 15. La Ciran. 16. Queguay limestone. 17. "Magellanian Beds." 18. Rio Cóndor ("minas de Carbón"). 19. Pachitea.


12
15
13
19
1a
1
4
2
5
3
16
11
7
6
11a
14
8
9
10
17
18

middle Miocene age overlying the Queguay limestone, but in certain places where erosion has destroyed the Queguay, the base of Fray Bentos fillings touches the Asencio sandstone (Cretaceous). The "roof" of Fray Bentos is the Sangregorian, equivalent to the Entre Ríos Mesopotamian. "Palmiran," according to G. G. Simpson, is approximately contemporary with the Friasean.

FRIASEAN "COLLONCUREAN" *(Patagonia)*

The absence of terrestrial mollusks in the rich mammal-bearing Santa Cruz formation and, in general in the Miocene of Patagonia, is impressive. After the Eocene (Casamayor, Musters), the Strophocheilidae, the Bulimulidae, and Chilinidae did not appear again in the region, except for the living species of *Chilina* and a single *Bulimulus.* Evidently the migration of these mollusks northward occurred early in the Tertiary (Notes 25 and 46).

A unique species, *Diplodon rothi* Ihering, is known from Sierra Leleque, Nahuel Huapi region, in Chubut, and was collected by S. Roth in 1898. The strata were recognized by Feruglio (1949) as belonging to the "Colloncurense," which Feruglio, as well as Kraglievich (1930) and G. G. Simpson (1940), consider to be upper Miocene (Note 25). The "Capas de Chichinales" on eastern Patagonia are, also according to Simpson, "more or less of this age but are still dubious" (Note 47).

A species of "*Corbicula*" was found in western Argentina, from the Calchaquian ("Estratos Calchaqueños"), usually included in the Araucanian, of the Santa María Valley and Fiambalá Bolsón, Catamarca. The species was never described, but in the literature it was often called *C. stelzneri* (Note 21).

MIOCENE FOSSILS

Diplodon guaranianus biblianus (Marshall)	Ecuador
Diplodon liddlei Palmer	Ecuador
Diplodon rothi Ihering	Patagonia
Monocondylaea azoguensis Palmer	Ecuador
Monocondylaea pacchiana Palmer	Ecuador
Anodontites olssoni Palmer	Ecuador
Fossula derbyi (Ihering)	Brazil
Neocorbicula cojitamboensis (Palmer)	Ecuador
Neocorbicula pacchiana (Palmer)	Ecuador
Neocorbicula stelzneri Parodiz	Argentina

Cyclodontina dentata (Wood)	Uruguay
Strophocheilus globosus (d'Orbigny)	Uruguay
Strophocheilus charruanus (Doello-Jurado)	Uruguay
Strophocheilus oblongus haemastomus (Scopoli)	Uruguay
Bulimulus fazendicus Maury	Brazil
Potamides maracaibensis Willston	Colombia
Potamides bolivariensis Weisbord	Colombia
Potamolithoides biblianus (Marshall & Bowles)	Ecuador
Poteria bibliana (Marshall & Bowles)	Ecuador
Doryssa bibliana (Marshall & Bowles)	Ecuador
Aylacostoma peyeri dickersoni (Palmer)	Ecuador

PLIOCENE

Most of the known Pliocene fresh-water mollusks from South America were found by J. H. Orton in 1867, in the Pebas formation of the Ambicayu River near its confluence with the Marañon, in the Iquitos region of Peru (Note 19). Some of them were described in 1869 by Gabb, in 1871-74 by Conrad, and in 1878 by Boettger. De Greve (1938) and Pilsbry (1944) increased the knowledge of that fauna. Other deposits from western Brazil with similar species (Note 56) were formerly included within the Pebas Group but lately have been recognized to be as modern as Pleistocene or Holocene. From the Canoa formation (marine) of Ecuador, a single land snail was included by Pilsbry *(Porphyrobaphe).* Among the new genera created by Conrad, some, as *Cyclocheila* or *Liosoma*, are almost impossible to identify.

The Peruvian fauna studied by Pilsbry was collected by J. T. Singewald in 1926, in the "Red Beds" of the Pachitean River between San Antonio and Santa Isabel. "All these deposits appear to have been laid down under estuarine conditions, perhaps roughly comparable to the estuary of the Rio de la Plata" (Pilsbry 1944:143).

On the eastern side of the continent this type of fauna is unknown. In Uruguay the Pliocene is mostly marine at Punta Gorda and at Chuy. Deposits of fluvial or aeolic origin are found on the Uruguay River (Salto sandstone), but because of intensive disintegration the outcrops have very limited extension, bearing no fossils. In the Entre Ríos formation on the Paraná River, in Argentina, fresh-water and land mollusks are sometimes found mixed with the marine (Mesopotamian-Entrerrian).

The Entre Ríos formation had a wide development. In addition to those strata well known in northern Patagonia (Note 20) and Paraná,

others were revealed in several deep perforations near the cities of Buenos Aires and La Plata. The fossils of the latter are similar to those of Paraná, as were others found in eastern Uruguay at Chuy, on the Brazil-Uruguay border. On the west shore of the Paraná, at Santa Fe, the Entre Ríos formation is deeply buried under thick, late Pliocene and Pleistocene sediments, while on the east side the cliffs, especially at Paraná, rise to more than 200 feet as the result of a fault of great magnitude, produced in the Pleistocene, along the scar of an old diaclase. Those sediments of Uruguay at Chuy also are deeply buried. The Paraná cliff represents the horst. The Paraná River, which apparently was previously united to the Uruguay, turned east and then south in the graben. It was at that time that the present system of La Plata River drainage came into existence. The Paraná fault, in Argentina, Uruguay, and Brazil, is synchronous with that of the Magdalena River in Colombia.

RIO NEGRO SANDSTONE AND ARAUCANIAN *(Patagonia)*

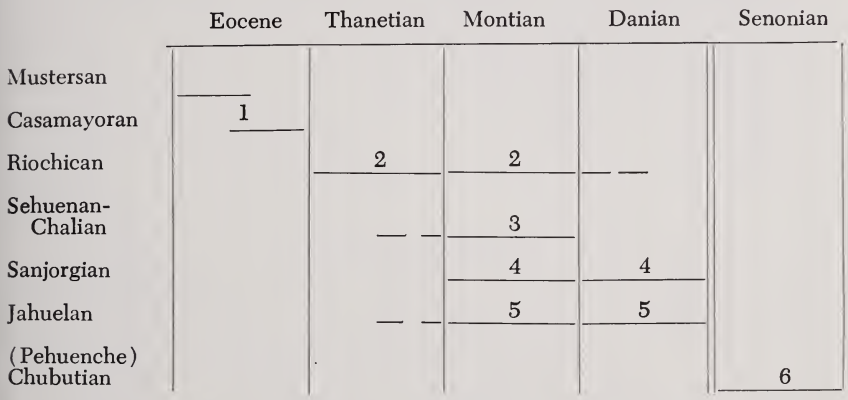
The "Rionegrense," or "Areniscas del Río Negro" of authors, is a lateral equivalent of the marine "Entrerrian," perhaps relatively younger. Usually it was placed at the top of the Entre Ríos formation following the Mesopotamian (= "Entreriense"). It presents marine as well as continental facies (Note 20). The conclusion reached by Feruglio (1949) after careful examination of the "Rionegrense" in its type locality (Golfo Nuevo, Chubut) is that a defined limit for it cannot be traced, but that there is very slow intergradation between Entrerrian and Rionegran. Fifteen of the 19 species indicated for the Rionegran are also found in the Entrerrian. From the mouth of the Río Negro to Puerto Piramides the Entrerrian increases in thickness in the same proportion as the Rionegran decreases, and in paulatine transition the sandy silts of the Rionegran fill the eroded surface of the Entre Ríos formation.

In Patagonia the Rionegran contains *Diplodon diluvii* (d'Orbigny), and at its corresponding level of Paraná, *Diplodon fraus* Ihering and *Corbiculella tenuis* Ihering. In the Patagonian sequence the Entre Ríos formation is followed by the Araucanian with several marine terraces in Chubut and Santa Cruz. The lower terrace at Sierra Laziar (Ameghino's "Laziarense") contains *Neocorbicula salobris* Ihering (Note 20).

In northwest Argentina, from strata of the "Andean or Subandean Tertiary" of Salta, Feruglio found casts of land snails of the genus

Epiphragmophora, which also lives abundantly in the region (Note 22).

TABLE 1. PALEOCENE AND EOCENE STRATIGRAPHY IN PATAGONIA



1,2 Terrestrial. Pan-Casamayoran fauna.
3 Fresh and brackish-water, (Jahuelan) mixed in the Sanjorgian strand. Lower section (Chalian) with fossil flora. In Chubut corresponding to "Banco Negro."
4 Marine. Began relatively earlier in the North (Roca) than in the South Salamanca). Both faunas very similar. Upper limit not well defined and grades into Jahuel.
5 Fresh-water. Widespread along the Sanjorgian strand and N.W. to Mendoza.
6 Widespread and varied terrestrial and marine Cretaceous: "Strata with Dinosaurs," Cazadorian, Lefipan, Ortizan, and others.

PLIOCENE FOSSILS

NORTHWEST SOUTH AMERICA

Diplodon singewaldi (Marshall)
Diplodon bassleri (Marshall)
Diplodon gardnerae (Marshall)
Tropidebora tertiana (Conrad)
Toxosoma eborescens (Conrad)
Hydrobia dubia Gabb
Hydrobia ortoni Gabb *(Dyris)*
Liris laqueata (Conrad)
Dyris gracilis (Conrad)
Liris minuscula (Gabb)
Liris tuberculata de Greve
Aylacostoma sulcatus (Conrad)
Aylacostoma peyeri (de Greve)
"Planorbis" pebasana Conrad

SOUTH AND SOUTHEAST SOUTH AMERICA

Diplodon chilensis patagonicus (d'Orbigny)
Diplodon fraus Ihering
Diplodon diluvii (d'Orbigny)
Neocorbicula salobris (Ihering)
Corbiculella tenuis Ihering
Epiphragmophora feruglioi Parodiz

TABLE 2. EOGENE CORRELATIONS

		COLOMBIA	N. ARGENTINA PERU BOLIVIA	CHILE	ARGENTINA, PATAGONIA, TIERRA DEL FUEGO		BRAZIL	URUGUAY
MIOCENE		Real Series	Biblian		Santacruzian		Itaborai II	Fraybentosan
OLIGOCENE	Second phase Andean uplift	Laciran (Colorado) Goajira	Upper Zorritosan	Navidean	Colhuehuapian Magellanian Deseadan			Queguayan
		Mugrosan	Lower Zorritosan		(Río Cóndor)	Pan-Casamayoran Faunas		
EOCENE		Uriba ? Corrosan Guaudas ?	Lobitosan Samanan	(Pre-Navidad) Concepcionan	Mustersan		(Maria Farinha)	
		Toro Lisama	Upper Negritosan	Boqueronian	Casamayoran			
PALEOCENE	First phase Andean uplift	Umir ?	Chiococan ? Lower Negritosan Mirafloran Pucan Sta. Barbara Upp. Pachitean	Lonquimay	Riochican Sanjor- gian	Salamancan Rocanean Sehuenan	Itaboraian I Bahian	
				Boca-Levu	Jahuelan		. . .	
SENONIAN		Palmiran	Lower Puca Pirgua Lower Pachitean	Quiriquinan	"Pehuenche"	Cazadorian Lefipan	Bauruan Gramamean	Guichonan Asencionan

Transitional Marine Fauna

TABLE 3. NEOGENE CORRELATIONS

	COLOMBIA VENEZUELA	PERU ECUADOR BOLIVIA	ARGENTINA N.W.	ARGENTINA Central & S.	URUGUAY	BRAZIL
PLEISTOCENE	Magdalenan (Abisinian)	Talaran, Mancoran, Salinan (Tablazos); Tarijan ? . . . Uquian		Querandinan, Belgranan, Bonarean, Ensenadan (Post-Pampean); Pampean	Querandinan; Post-Azaratian	Itaborai III; "Sambaquis"; Lagoa Santa
PLIOCENE	Mesian; Marenian; Maiquetian	Canoan; Pebas (Red Beds)	Chapadmalalan; Montehermosan; "Subandean Tertiary"; Tunuyan; Huayquerian (Araucanian)	Entrerrian (=Rionegran) (Arauco-Entre Ríos Group)	Azaratian; Saltoan; Chuyan . ? .	Rio Branco; Pirapenasan; Maraunan
MIOCENE	Catian; Hondanian; Monagan, Sta. Inez; Real series: Sogomosan, Oponcitonian, Zarazan	Azoguean; Progresan, Cuencan, Biblian (Azogue-Cuenca Group); Desaguadero	Mesopotamian (=Paranan); Chiquimil; Chasicoan (Santamarian ?); Calchaquian (Mayan); Chichinales; Friasean; Magellanian, Santacruzian, Patagonian	Camachan; San Gregorian ? . . . Pirabasan	Fraybentosan; Santalucian ?	Itaborai II
OLIGOCENE	Laciran	Pachitea; Lower Zorritosan	Colhuehuapian		Queguay	

Distributional Data

Localities

ALEMANIA

Town in south-central Salta, Argentina.

AMENIDA LAKE

8 mi. S. of Sehuen River, E. of Lake Viedma and S.E. of Mata Amarilla, Santa Cruz, Argentina.

AZOGUES

Town in Canar province, W. of Azogues River and E. of Cerro Abuja, Ecuador.

BAHIA

(= Salvador) N.E. Brazil

BAJO AMENIDA

(see Santa María Valley)

BAJO SANTA ROSA

Lowland in the Negro River Valley, S.E. of Bajo de los Menucos, halfway between Choele-Choel and Falckner, N. Patagonia, Argentina.

BARRANCAS AL NORTE

("Falaises du Nord" d'Orbigny) northern cliffs of the lower Negro River in N. Patagonia.

BIBLIAN

Few miles N.E. of Azogues and S.W. of Canar and Cerro El Shalal (northern area of the Biblian-Cuenca region), Ecuador.

BIO BIO RIVER

(Valley of Bío Bío) S. central Chile, running from Lonquimay N.W. to Concepción.

CABO BLANCO

Coast of Venezuela, 4 mi. W. of La Guaira.

CALAVERA, ARROYO

(See Santa María Valley)

CAMPO DURAN (Oil fields)

N. of Aguray and Tartagal, N.E. of province of Salta, Argentina, near the Bolivian-Argentine border.

CANADON BLANCO

Between the Senguerr and Chubut rivers, Chubut, Argentina.

CANADON HONDO

Between Lake Colhue-Huapi and Salamanca, on the Chico River, Chubut, Argentina.

CANADON VACA

W. of the Niemann Pass of the Chico River, Chubut, Argentina.

CARBAJAL

S.W. of Rosario de Lerma, short distance from Lerma *pucará,* S. of Salta City, Argentina.

CASAMAYOR, PUNTA
Southern coast of San Jorge Gulf, N. of Mazaredo, Argentina.

CERRO BAYO DE ESPERANZA
Southwest Mendoza, Argentina.

CHAPADMALAL
Town and Creek south of Mar del Plata, Prov. Buenos Aires, Argentina.

CHICO RIVER
Affluent of Chubut River, running N.E. from Colhue-Huapi, eastern Chubut, Argentina.

COLHUE-HUAPI LAKE
S.E. of Chubut (Patagonia), Argentina, E. of Musters Lake.

COLLONCURA RIVER
Affluent of Limay River, southern Neuquén, Argentina. Also town between San Martín de los Andes and Sanico.

COLORADO
Town and river, in northern Rio Negro province, Argentina. The river marks the physiographic limit between the northern Patagonian region and the pampas. Also river in the Magdalena Valley, Colombia.

CONDOR RIVER
Western Tierra del Fuego, S. of Bahia Inútil, across Dawson I., Chile.

CUAREIM RIVER
Stream dividing N.W. Uruguay from Brazil.

CUENCA
Northern Ecuador, N. of Matadero River.

EL MOLINO
S.W. of Miraflores and Tarapaya, in the vicinity of Potosí, Bolivia.

FRAY BENTOS
Town on the Uruguay River, N.W. of Mercedes, Uruguay.

FRESNO MENUCO
(See General Roca)

GAIMAN NUEVO
Town on the Chubut River, W. of Trelew, Chubut, Argentina.

GENERAL ROCA
Town on the upper Negro River Valley, E. of confluence with Limay River, N. Patagonia, Argentina (formerly known as Fresno Menuco).

GUANABARAS
(See Oponcito River)

IMBABURA
River, and province in northern Ecuador.

ISLA DESEADO
A large island in Santa Cruz, Argentina, during Paleocene, in the San Jorge Sea.

ITAIMBE
Municipality of Taquiritinga, São Paulo, Brazil.

ITIYURO RIVER
Northernmost Salta, near Campo Duran, Argentina; close to Bolivian border.

JAHUEL (or JAGUEL)
Down the eastern slope of Sierra Auca Mahuida and Bajo del Palo, S. of Colorado River, Neuquén, Argentina.

LA CIRA
Near Guanabaras, at the bend of the Oponcito River, N.W. Colombia.

LAGUNITAS
5 mi. S. of Punta Pariñas and Negritos, N.W. Peru.

LA PAZ
Town on the Paraná River, Entre Ríos province, Argentina.

LAZIAR, SIERRA
50 km. N.W. of Puerto Deseado, Santa Cruz, Argentina.

LA QUIACA
Town on the Argentine-Bolivian border, province of Jujuy, Argentina.

LELE (or LELEQUE), ARROYO
N.W. Chubut, Argentina, at foot of Sierra Leleque, halfway between Ñorquincó and Esquel.

LENZA NIYEU
Lowlands of Río Negro, (N. Patagonia), Argentina.

LEPPA, ARROYO
W. Chubut, at foot of Sierra Leleque.

LLANO RIVER
Affluent of the Magdalena River, Colombia.

LOS CORROS
On the Sogamoso River, Magdalena Valley, Colombia.

MALLIN BLANCO
E. of Languiñeo, W. central Chubut, Argentina.

MAIMARA
5 km. S. of Tilcara, N. of province of Jujuy, Argentina.

MATA AMARILLA
Southern Santa Cruz, on the Sehuen (or Chalia) River, Argentina.

MERCEDES
Town in S.W. Uruguay, S. of Fray Bentos and N. of Palmitas.

MIGUEZ
Town in Dept. of Canelones, southern Uruguay.

"MINAS DE CARBON"
At Condor River, western Tierra del Fuego, Chile.

MIRAFLORES
N.W. of Potosí, and N. of Tarapaya, Frias province, Dept. Potosí, Bolivia.

MONSERRATE
10 km. N. of Bahia, Brazil.

MUGROSA
30 km. E. of Magdalena River, S. of Barranca Bermeja, Colombia.

NAHUEL NIYEU
N.W. of Valcheta, prov. of Río Negro, Argentina.

NEGRITOS
Northern coast of Peru, near Talara and S. of Lobitos, Piura province.

OPONCITO RIVER
Affluent of the Magdalena River near Guanabaras and S. of Sogamoso, Colombia.

PACHITEA RIVER
Affluent of the Ucayali River, province Huanaco, central Peru.

PALOMETAS RIVER
Affluent of the Piray River in Santa Cruz de la Sierra, Bolivia.

PALMITAS
Town in the Dept. of Soriano, Uruguay.

PAMPA DE NAHUEL HUAPI
S.E. of Cerro Bernal, near Nahuel Huapi Lake, Neuquén, Argentina.

PARANA (and Bajada de Paraná, d'Orbigny)
Capital of Entre Ríos Province, on the Paraná River, Argentina. (Paraná ravines.)

PAUCAPARTA
On the Marañon River, N.W. Peru.

PEBAS
Near Iquitos, in eastern Peru.

POTRERO, ARROYO
W. of Cojitambo, in the vicinity of Cuenca, Ecuador.

POYUCA STATION
85 km. N. of Bahia, Brazil.

PUESTO DE LOS CHINOS
Near Iquitos, in eastern Peru.

PUNTA BLANCA
West of Guayaquil, Ecuador.

PUNTA PARINAS
Westernmost Peru, south of Negritos.

PUNTA SAL CHICO
Western Peru, near Negritos.

QUEBRADA MARE ABAJO
Gorge in the Cabo Blanco area, northern Venezuela.

QUEBRADA PACCHA
Gorge near Biblian, in province of Azuay, Ecuador.

QUEGUAY RIVER
Affluent of the Uruguay River, N. of Paysandú, Uruguay.

QUEQUEN SALADO RIVER (at IRENE)
100 km. W. of Quequén Grande River, southern Buenos Aires prov., Argentina. Irene is 40 km. N. from Atlantic coast.

SALAMANCA, PEAK
N. of Comodoro Rivadavia and W. of Puerto Viser and Punta Matalinares, on the San Jorge Gulf coast, Chubut, Argentina.

SANGUINETTO, BAHIA
Bay near Puerto Deseado, Santa Cruz, Argentina.

SAN JOSE DE ITABORAI
Municipality of Itaborai, State of Rio de Janeiro, Brazil.

SANTA MARIA DA BOCA DO MONTE
State of Rio Grande do Sul, Brazil.

SANTA MARIA VALLEY
Eastern Catamarca, Argentina along the 66° parallel. The town of Sta. Maria is 10 km. from the Tucumán border and is S. of Quilmes. Includes loc.: Arroyo Calavera, Bajo Amenida, Calimonte, and San José.

SEHUEN RIVER
Also called Chalia. Southern Santa Cruz, Argentina.

SENGUERR RIVER
Ending in Lake Musters, southern Chubut, Argentina.

SOGAMOSO RIVER
Affluent—eastern side—of the Magdalena River, running from the eastern cordillera, Colombia.

SUCIO RIVER
A branch of Llano River, S.E. of Infantas, Magdalena Valley, Colombia.

SUNGARILLO
Gorge in the Pachitea River, Peru.

TINGUIRIRICA
River, and Pass, of the Andes, province of Colchagua, Chile, near border with Argentina at Mendoza.

TRAPALCO, AGUADA
Lowland near Bajo Santa Rosa, province Río Negro, Argentina.

TRES CRUCES
Railroad junction near La Quiaca, province of Jujuy, Argentina.

TRINETRA, ARROYO
Near Nahuel Niyeu, Río Negro province, Argentina.

VALLE DE PAULA
E. of Arroyo Pacunto, an affluent of Bío Bío, between Gayetul and Lonquimay, Chile.

YAGUARETE CHICO, ARROYO
Creek near Fray Bentos, Uruguay.

YAVI
Town in province of Jujuy, Argentina, on the Argentina-Bolivia border.

ZOPFFS
Town in the Magdalena Valley, Colombia.

List of Species by Countries
North to South

Venezuela	
Potamides supersulcatus (Gabb)	Miocene
Pachychilus caboblanquensis Weisbord	Pliocene
Colombia	
Dorussa corrosensis (Pilsbry & Olsson)	Paleocene
Potamides mcgilli Pilsbry & Olsson	Eocene
Dyplocyma wheeleri Pilsbry & Olsson	Eocene
Sogamosa cyrenoides Pilsbry & Olsson	Eocene

Diplodon oponcitonis Pilsbry & Olsson	Oligocene
Diplodon latouri (Pilsbry & Olsson)	Oligocene
Monocondylaea marshalliana Pilsbry	Oligocene
Anodontites laciranus Pilsbry & Olsson	Oligocene
Lyrodes laciranus (Pilsbry & Olsson)	Oligocene
Pachychilus gracillimus Pilsbry & Olsson	Oligocene
Pyrgulifera avus (Pilsbry)	Oligocene
Aylacostoma sigmachilus (Pilsbry & Olsson)	Oligocene
Aylacostoma paleus (Pilsbry)	Oligocene
Aylacostoma eucosmius (Pilsbry & Olsson)	Oligocene
Aylacostoma mugrosana (Pilsbry & Olsson)	Oligocene
Aylacostoma waringi (Pilsbry & Olsson)	Oligocene
Aylacostoma laevicarina (Pilsbry & Olsson)	Oligocene
Poteria bibliana (Marshall & Bowles)	Miocene
Ecuador	
Diplodon liddlei Palmer	Miocene
Diplodon guaranianus biblianus (Marshall)	Miocene
Monocondylaea azoguensis Palmer	Miocene
Anodontites olssoni (Palmer)	Miocene
Neocorbicula pacchiana Palmer	Miocene
Neocorbicula cojitamboensis (Palmer)	Miocene
Potamolithoides biblianus Marshall & Bowles	Miocene
Doryssa bibliana (Marshall & Bowles)	Miocene
Aylacostoma peyeri dickersoni (Palmer)	Miocene
Porphyrobaphe iostoma bilabiata Pilsbry	Pliocene
Peru	
Pachychilus dimorphica (Woods)	Paleocene
Pachychilus bicarinatus (Fritzsche)	Paleocene
Morgania magna Woods	Eocene
Morgania costata Woods	Eocene
Neocorbicula sp.	Eocene
Potamides lagunitensis (Woods)	Eocene
Potamides occidentalis Woods	Eocene
Lagunites peruvianus (Woods)	Eocene
Ampullaria manco (Pilsbry)	Oligocene
Aylacostoma pictus (Pilsbry)	Oligocene
Hannatoma gesteri Hanna & Israelski	Oligocene
Aylacostoma sulcatus (Conrad)	Pliocene
Aylacostoma tuberculifera (Conrad)	Pliocene
Aylacostoma peyeri (de Greve)	Pliocene
Dyris ortoni (Gabb)	Pliocene
Dyris gracilis Conrad	Pliocene
Liris minuscula (Gabb)	Pliocene
Liris laqueata Conrad	Pliocene
Liris tuberculata de Greve	Pliocene
Tropidebora tertiana (Conrad)	Pliocene

Toxosoma eborea (Conrad)	Pliocene
Taphius pebasana (Conrad)	Pliocene
Cirrobasis venusta Conrad	Pliocene
Diplodon gardnerae (Marshall)	Pliocene
Diplodon singewaldi (Marshall)	Pliocene
Diplodon bassleri (Marshall)	Pliocene
Triplodon longula (Conrad)	Pliocene
Leila capax (Conrad)	Pliocene
Bolivia	
Neocorbicula dormitator (Pilsbry)	Paleocene
Eriphyla miraflorensis Parodiz	Paleocene
Valvata humilis Fritzsche	Paleocene
Lioplacodes bolivianus Parodiz	Paleocene
Doryssa andicola Pilsbry	Paleocene
Potamides potosensis (d'Orbigny)	Paleocene
Taphius boliviensis (Fritzsche)	Paleocene
Taphius molino (Pilsbry)	Paleocene
Pisidium sp.	Paleocene
Brazil	
Paxyodon priscus (Ihering)	Paleocene
Anodontites totiumsanctorum (Hartt)	Paleocene
Anodontites hartti (White)	Paleocene
Anodontites mawsoni (White)	Paleocene
Anodontites allporti (White)	Paleocene
Sphaerium altivum White	Paleocene
Lioplacodes williamsi (Hartt)	Paleocene
Lioplacodes lacerdae (Hartt)	Paleocene
Pachychilus terebriformis (Morris)	Paleocene
Taphius monserratensis (Hartt)	Paleocene
Fossula derbyi (Ihering)	Miocene
Strophocheilus sanctijosephi Maury	Miocene
Bulimulus fazendicus Maury	Miocene
Itaboraia lamegoi Maury	Miocene
Brasilennea arethusae Maury	Miocene
Chile	
Diplodon burckhardti (Mayer-Eymar)	Eocene
Diplodon transandinus Parodiz	Eocene
Paleoanculosa araucana (Philippi)	Eocene
Potamolithus capitatus (Mayer-Eymar)	Eocene
Chilina fischeri (Mayer-Eymar)	Eocene
Ancylus humboldti (Mayer-Eymar)	Eocene
Neocorbicula sp.	Eocene
Diplodon nordenskjoldi Steinmann & Wilckens	Oligocene
Diplodon chilensis (Hupe)	Oligocene
Neocorbicula chilensis (Soot-Ryen)	Miocene

Uruguay	
Lymnaea klappenbachi Parodiz	Miocene
Taphius walteri Parodiz	Miocene
Strophocheilus globosus (Martens)	Miocene
Cyclodontina dentata (Wood)	Miocene
Strophocheilus charruanus (Frenguelli)	Oligocene
Argentina	
Diplodon colhuapiensis Ihering	Paleocene
Diplodon bondenbenderi Doello Jurado	Paleocene
Diplodon pehuenchensis Doello Jurado	Paleocene
Eriphyla sehuena (Ihering)	Paleocene
Neocorbicula pehuenchensis Doello Jurado	Paleocene
Neocorbicula sp.	Paleocene
Lioplacodes feruglioi Parodiz	Paleocene
Lioplacodes wichmanni Doello Jurado	Paleocene
Potamolithus windhauseni (Parodiz)	Paleocene
Paleoanculosa bullia (Ihering)	Paleocene
Paleoanculosa macrochilinoides (Doello Jurado)	Paleocene
Paleoanculosa patagonica Parodiz	Paleocene
Doryssa maimarensis (Bonarelli)	Paleocene
Pyrgulifera sehuena Parodiz	Paleocene
Pyrgulifera feruglioi (Bonarelli)	Paleocene
Aylacostoma striata (Bonarelli)	Paleocene
Aylacostoma brackebuschi (Bonarelli)	Paleocene
Potamides patagonensis Ihering	Paleocene
Potamides doelloi (Bonarelli)	Paleocene
Potamides chaliana Parodiz	Paleocene
Potamides turgidus (Bonarelli)	Paleocene
Potamides potosensis (d'Orbigny)	Paleocene
Potamides decarlesi (Bonarelli)	Paleocene
Valvata yaviana Fritzsche	Paleocene
Valvata satira Fritzsche	Paleocene
Physa wichmanni Parodiz	Paleocene
Physa doeringi Doello Jurado	Paleocene
Strophocheilus chubutensis Ihering	Paleocene
Strophocheilus hauthali Ihering	Eocene
Thaumastus patagonicus Parodiz	Eocene
Paleobulimulus eocenicus Parodiz	Eocene
Chilina stenopstylus Parodiz	Eocene
Diplodon burckhardti (Mayer Eymar)	Eocene
Diplodon chilensis patagonicus (d'Orbigny)	Oligocene
Diplodon rothi Ihering	Miocene
Neocorbicula stelzneri Parodiz	Miocene
Neocorbicula tenuis (Ihering)	Pliocene
Neocorbicula salobris (Ihering)	Pliocene
Diplodon diluvii (d'Orbigny)	Pliocene
Diplodon fraus Ihering	Pliocene

Chilina antiquata d'Orbigny	Pliocene
Epiphragmophora feruglioi Parodiz	Pliocene
Strophocheilus lutescens dorbignyi (Doering)	Pliocene

Paraguay and the Guianas are unlisted, as non-marine fossil mollusks of these countries are practically unknown. In Peru and Argentina there is a complete sequence — although not for all groups — from Paleocene to Pliocene. More species are listed for these countries because their geology and paleontology have been better explored. Colombia and Chile follow in this respect. In Ecuador and Venezuela the records go back only to the Miocene, and in Bolivia the only better known Tertiary is the Paleocene. Brazil as well as Uruguay have only incomplete records regarding fresh-water fossils. There is a very large inland area from Paraguay northwards, between longitudes 48° and 64° W., from which we do not have fossil records, and its exploration might increase our present knowledge greatly. The preceding lists show that many of the older deposits, such as those of the Paleocene and Eocene, are concentrated along, or are relatively closer to, the Pacific border of the continent, immediately east or west of the Andes. This is especially true in the south, which gives support to the theory that the great faunal migration from North to South America at the end of the Cretaceous took place along some eastern Pacific area of land communication. Contrarily, areas bordering the Atlantic are very poor in Eogene fauna. The early Neogene is represented, — but not abundantly by fresh-water mollusks — in all countries except Bolivia. That period was largely one of terrestrial sedimentation, with great changes in continental water basins, followed by an intensive expansion and adaptive radiation of many forms, from south to north and vice versa. These forms became established in the Recent fauna and were joined by some new immigrants from Central America in the Pliocene.

Systematic Review

PELECYPODA

Superfamily Unionacea

Family Hyriidae Swainson, 1840 [Hyriia-nae]

Subfamily Hyriinae (restricted Parodiz & Bonetto, 1963)

Tribe Diplodontini

The tribe Diplodontini differs from other Hyriinae (Prisodontini and Castalini) by its always-present radial ribs on the umbo, sometimes extending as far as the middle area of the shell (Pilsbry, Ihering, Ortmann, and Marshall agree on the primitiveness of this character); and by its non-alate dorsal area, although in the subgenus *Rhipidodonta* some species are subalate but with the posterior ridge less developed than in *Prisodon* or *Castalia.*

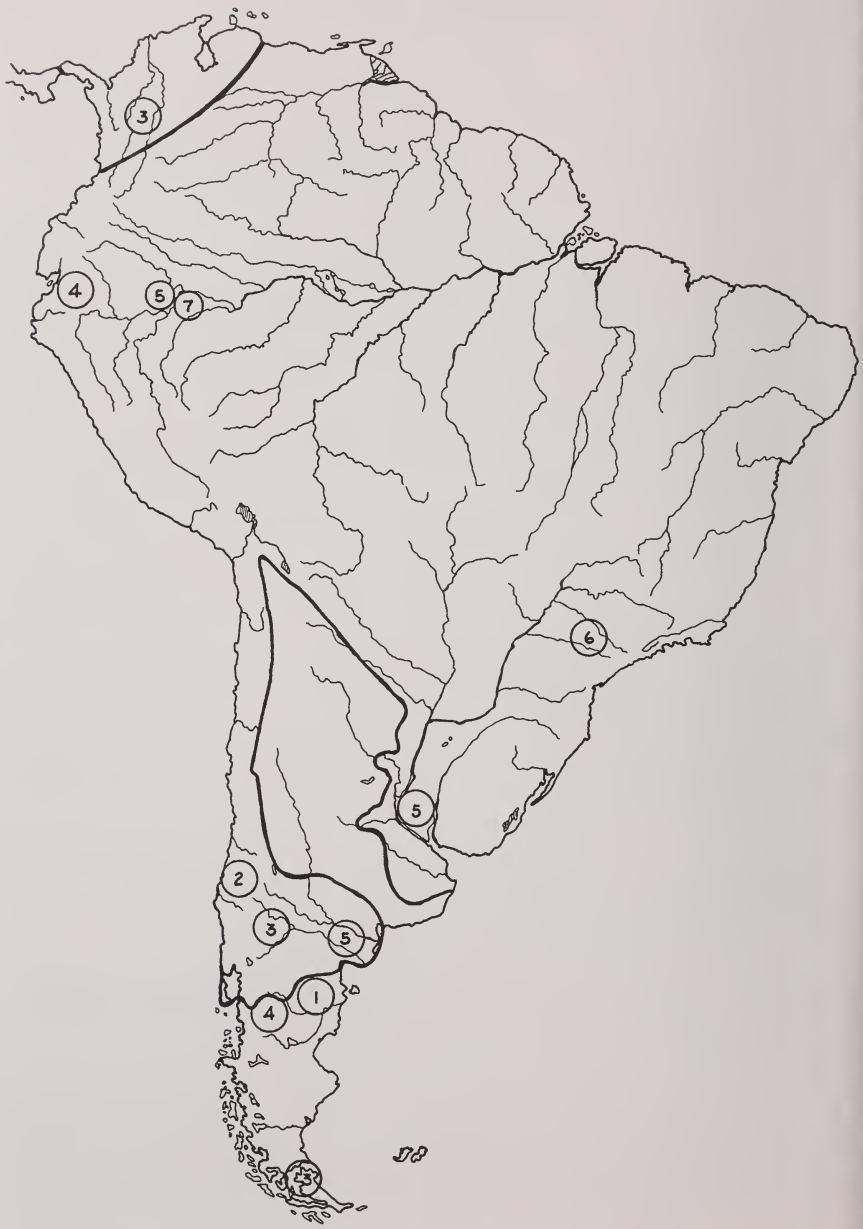
Genus *Diplodon Spix*, 1827

Type: *D. ellipticum* Spix

Iridea Swainson, 1840.
Prodiplodon and *Eodiplodon* Marshall, 1928.
Antediplodon Marshall, 1929.
Ecuadorea Marshall, 1932.
Castalioides Marshall, 1934.
Schleschiella Modell, 1950.

The living species of *Diplodon* present extraordinary ecological and individual variations, recurring and mixed among the populations and demes. Taxonomy at the species level used to be confused, but recently has been partially resolved by the embryological studies of Bonetto. In general, when several nominal species, closely related, are grouped together as polytypic, they conform to the concept of *rassenkreis,* or may constitute "superspecies" (see Note 38).

Describing the oldest known species, from the Triassic of Pennsylvania (Note 23), Pilsbry used *Diplodon, sensu lato,* without subgeneric denominations, well aware that the bases for clear subdivisions were still lacking. In the case of only the species from the Oligocene of


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Colombia, that author indicated *Rhipidodonta* because of the conspicuous similarity with living species of this group.

The most reliable factor for dividing *Diplodon* into groups consists in the parasitic or non-parasitic condition of the larvae. Although this is unobservable in fossils, groups of species may be recognized by shell characters, in spite of the difficulties presented by the gradual, intergraded variations, as follows:

1a. With parasitic glochidia *Diplodon, sensu stricto* 2

1b. Glochida non-parasitic Subgenus *Rhipidodonta* 3

2a. Shell elongated, compressed laterally, central costulae with marked convergence and tendency to cross, forming thick folds or nodules. External branchiae higher than internal and marsupium anteriorly placed *D. chilensis* group

2b. Variable in length, diameter and altitude. Sculpture less convergent, not crossed. External branchiae of same height as internal. Marsupium central or with posterior gravitation .. *D. rhuacoicus* group

3a. Size and shape variable but generally more rounded. Sculpture moderately convergent, less prominent than in 3a but more than in 2. Hinge very variable *D. paranensis* group

3b. Small but very thick and more inflated. Strong V-shaped sculpture extended toward the middle of the shell or beyond, with several central and convergent chevron-like costulae. Hinge thick and strong *D. guaranianus* group

Although many species can be classed in these groups there are others of intermediate type that defy clear positioning. Thus no sharply defined division can be made between 2a and 2b or between 3a and 3b, and they cannot be treated subgenerically.

Rhipidodonta Morch, 1853, includes as synonyms:

Cyclomya Simpson, 1900
Bulloideus Simpson, 1900
Ecuadorea and *Schleschiella*

Schleschiella in an assemblage of unrelated species, and in its type, *D. burroughianus* Modell included the form *rhuacoicus*, which has a parasitic glochidia, as well as *D. parallelipipedon.*

MAP 2

Heavy lines indicate distributional limits of living Hyriidae in South America. Populations absent or rare beyond northwest line, within the central Pampas-Chaco region, and in the southern end of the continent. Numbers indicate fossil localities: *Diplodon*, 1. Paleocene, 2. Eocene, 3. Oligocene, 4. Miocene, 5. Pliocene; *Paxyodon*, 6. Paleocene; *Triplodon*, 7. Pliocene.

Between 1928 and 1934 Marshall created five generic names for fossil species of South and North America:

Prodiplodon (1928:1). Sculpture of V-shaped undulations, "nesting" with each other, "distinctly related to *Diplodon* and *Hyria*."

Eodiplodon (1928:4). With V-shaped undulations broken into nodules, "related to *Diplodon*."

Antediplodon (1929:4). Elongated; sculpture of fine clear-out direct riblets, radiating.

Ecuadorea (1932:5). Radial ribs in V-pattern, each V nesting in a succeeding one. Posterior dorsal area with several plica crossing obliquely.

Castalioides (1934:78). There is no substantial difference between its type and *Ecuadorea*.

The hinge of *Prodiplodon* is similar to that of the *D.chilensis* group [including *transandinus*, and *ellipticus* (Note 37)], and there are no remarkable differences between *Prodiplodon* and *Eodiplodon*. The name *Antediplodon* was used by subsequent authors for older species of the Mesozoic of North America. Revising the types of the Triassic species from Pennsylvania, I found that they do not agree with the designated type of *Antediplodon* (*Unio dumblei* Simpson) from the upper Tertiary of Texas which, on the other hand, resembles *D. parallelipipedon* or *D. fraus*. If this relationship is confirmed by further discoveries, then the genus *Diplodon* persisted in North America until the Tertiary. *Ecuadorea*, from the Miocene of Ecuador, was created for a species that is a form of one still living, *D. guaranianus*. On the basis of these data I shall refer here to all the fossil species under the global name of *Diplodon* (except for *Rhipidodonta*), following Pilsbry's conservative and sound procedure.

Comparison of the fossil records of *Diplodon* with the recent species and their distribution suggests the following conclusions:

Fossils, from the Paleocene up, are more abundant in the western section of the continent; most living species are from the central and eastern section; the oldest South American fossils are from the southern region, becoming more abundant northward from middle to upper Tertiary; those of the Paleocene are related to the Triassic species of Pennsylvania; the ancient South American stock evolved into the Recent group of *D. guaranianus* and probably the non-parasitic condition of glochidia was a primitive character; Recent species of other groups derive from the *D. chilensis* stock. which is also linked to the Recent Hyriidae of Australia; migration of *Diplodon* from North to South America could not have taken place before the ending of the Cretaceous

(Note 57); the area for this migration was probably on land extension west of the present Pacific coast; between this land extension and the eastern mainland, a shallow sea existed; expansion to the north and northeast probably took place after this middle Tertiary.

The recognized fossil species are:

Paleocene

D. colhuapiensis Ihering
D. bondenbenderi Doello-Jurado
D. pehuenchensis Doello-Jurado
D. transandinus Parodiz

Eocene ?

D. burkhardti (Mayer-Eymar)

Oligocene

D. nordenskjoldi (Steinmann & Wilckens)
D. oponcitonis Pilsbry
D. latouri (Pilsbry)
D. chilensis patagonicus (d'Orbigny) – Recent

Miocene

D. guaranianus biblianus (Marshall)
D. liddlei Palmer
D. rothi Ihering

Pliocene

D. gardnerae (Marshall)
D. singewaldi (Marshall)
D. bassleri (Marshall)
D. fraus Ihering
D. diluvii (d'Orbigny)

Diplodon colhuapiensis Ihering
Plate 1, figs. 1-4

Ihering, 1903:217, fig. 2; 1907b:466; 1914:36.
Ameghino, 1906:47.

The original description of this species was very brief. The following is a complementary description based on revision of the type lot:

Shell of medium size, less compressed than *chilensis* or *transandinus*. Anterior margin low and rounded, posterior subangulated, suggesting it must have been thin and fragile, since in most of the specimens it is truncated. Dorsal margin concave in front of the umbo, with a sinus-like depression which makes the umbo appear higher. Remaining portion from middle to end almost straight; for that reason umbonal area in most specimens was preserved as inner cast, not showing radial sculpture, but rest of shell shows conspicuous lines of growth, with evidence of rugose surface, although not well marked as in *granosus* or *transandius*. Hinge not visible. All the specimens have both valves strongly cemented with gray sandstone matrix, and the fossils have a general black appearance, sometimes ferruginous as in *transandinus*.

In Ihering's 1914 catalogue, two lots are indicated:

a. From Colhue Haupi, Chubut, Cretaceous, "Salamanqueano," coll. Carlos Ameghino [1903], 3 specimens. Type.

b. From Sehuen River, Santa Cruz, "Upper Cretaceous," coll. S. Roth [1897?], 4 casts.

Roth's specimens from Sehuen were not found when I revised Ihering's collection, but in the "type lot" there were eight specimens instead of three, and I presume that both lots were mixed. With them was a label corresponding to Sehuen, indicating that the collector was Hauthal, not Roth. Ihering used to return part of the classified material to Ameghino, but a revision of the latter collections did not show *D. colhuapiensis*.

Identification and selection of the type (in CM) was possible by comparison of the actual dimensions and the published figure, which results in some peculiar findings (although the actual dimensions of the type are slightly smaller than those given in the original description: 51.5 mm. long, 30 mm. high, and diameter between valves 18 mm.). Ihering's handwriting on the label says: "*Diplodon diluvii* d'orb. Colhaupi [sic], formacion de *Pyrotherium*, C. Ameghino 1903" (Note 24).

The stratigraphic occurrences of this species are important to clarify the position of the Sehuenan. The original label notation "form. *Pyrotherium*" is undoubtedly wrong, because that stage (now Deseadan) is Oligocene and these *Diplodon* are older. It is not from Salamanca

PLATE 1

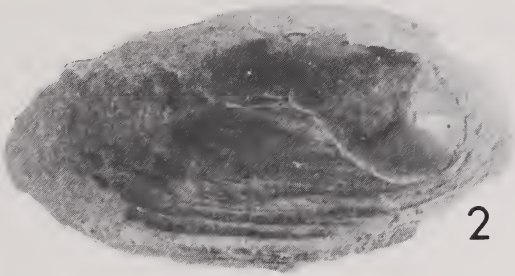
1-4. *Diplodon colhuapiensis* Ihering. 1, 3, 4. Type. 2. Paratype. 1, 2, 3., x1⅓; 4., x2.

5. *Diplodon pehuenchensis* Doello-Jurado. Type, x1 (from reproduction in Wichmann).

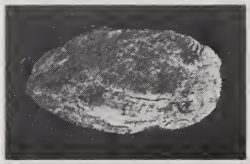
6. *Diplodon bondenbenderi* Doello-Jurado. Type, x1 (from reproduction in Wichmann).



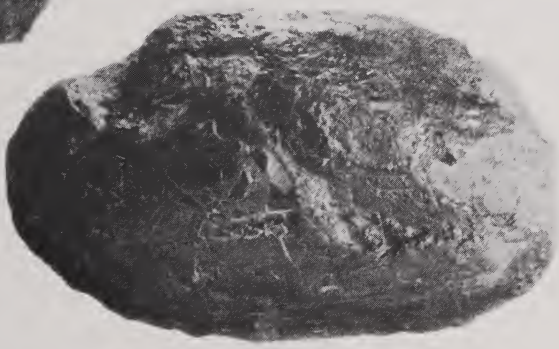
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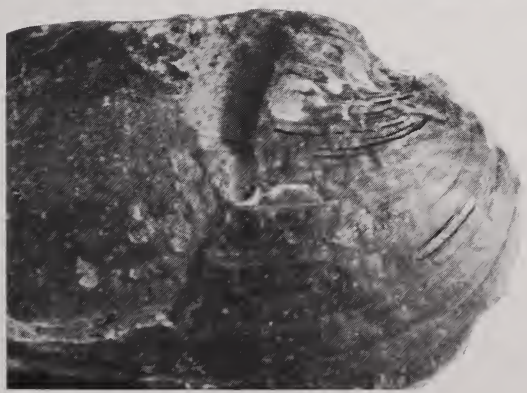


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either, as mentioned in the original description and in 1914, since that is a facies of the marine Sanjorge. The fresh-water equivalent of the Sehuenan, at Colhue Huapi, is upper Danian or Montain, representing a northern facies of the Jahuelan, somewhat contemporary with Simpson's Riochican. The strata were previously confused because at Colhue Huapi are found almost all the terrestrial formations from Paleocene to Oligocene, except Rio Chico which there is replaced by Jahuel. It is interesting that the geographical separation of *colhuapiensis* from other species of *Diplodon* took place because the region of Chubut and northern Santa Cruz was a large island (Windhausen's Isla Deseado) surrounded by the San Jorge Sea during the Eogene.

Diplodon bondenbenderi Doello-Jurado

Plate 1, fig. 6
Plate 2, figs. 4-7

Doello-Jurado, 1927:411, pl. 3, fig. 14-16, and pl. 4, fig. 18 of Wichmann's 1927 in the same journal.

Following is the complementary description (based on type lot):

Shell transversally shorter, higher, and more inflated than *colhuapiensis*. Anterior margin well rounded and ventral margin convex. Umbonal area prominent but its posterior slope not as strongly marked as in *pehuenchensis*. Umbo has very conspicuous radial sculpture, but not in front of it as in *pehuenchensis*. Hinge with the anterior and inferior teeth long and lamelliform, lacking lower laterals. In most of the specimens, with both valves cemented, the posterior end is fractured, but it is complete in the type (a single right valve) measuring 46 mm. x 30 mm. x 12.5 mm., slightly different from the dimensions indicated by its author (24 mm. to 28 mm. wide).

Type and paratypes (in CM) from Bajo Santa Rosa (S.E. of Bajo Menucos) about fifty miles S. of the Negro River of Patagonia, on the 40° parallel, collected by R. Wichmann 1926. Other specimens were found in nearby localities: high cliffs of Aguada Tapalcó, Nahuel Niyeu, and Arroyo Trinetra. Age Jahuelan, Danian. Specimens are abundant. Most of the "Unios" of Río Negro reported by geologists for the formerly called "Senoniano lacustre" belong to this species.

Diplodon pehuenchensis (Doello-Jurado)

Plate 1, fig. 5
Plate 2, figs. 1-3

Doello-Jurado, 1927:410, pl. 3, fig. 13, and pl. 4, fig. 20 of Wichmann.

This species was originally described as a "var." of *colhuapiensis,* but comparisons of the types revealed obvious specific differences. The type

is about half the size of *colhuapiensis,* more triangular posteriorly, with umbo closer to the anterior end and a very distinct ridge running between them. The concentric lines are less marked. Right shells of paratypes show the internal hinge with the lower lateral teeth well developed.

TYPE LOCALITY: Lowlands of Lenza Niyeu, province of Río Negro (Patagonia), Argentina, in the Jahuel formation. Type in CM. It is scarce and was found together with other abundant fresh-water shells of these strata, as *Physa, Viviparus,* and *Paleoanculosa.* It looks like a miniature of *D.parallelipipedon.* 25 mm. x 13.7 mm. x 7.3 mm.

Diplodon transandinus Parodiz

Plate 3, figs. 5-7

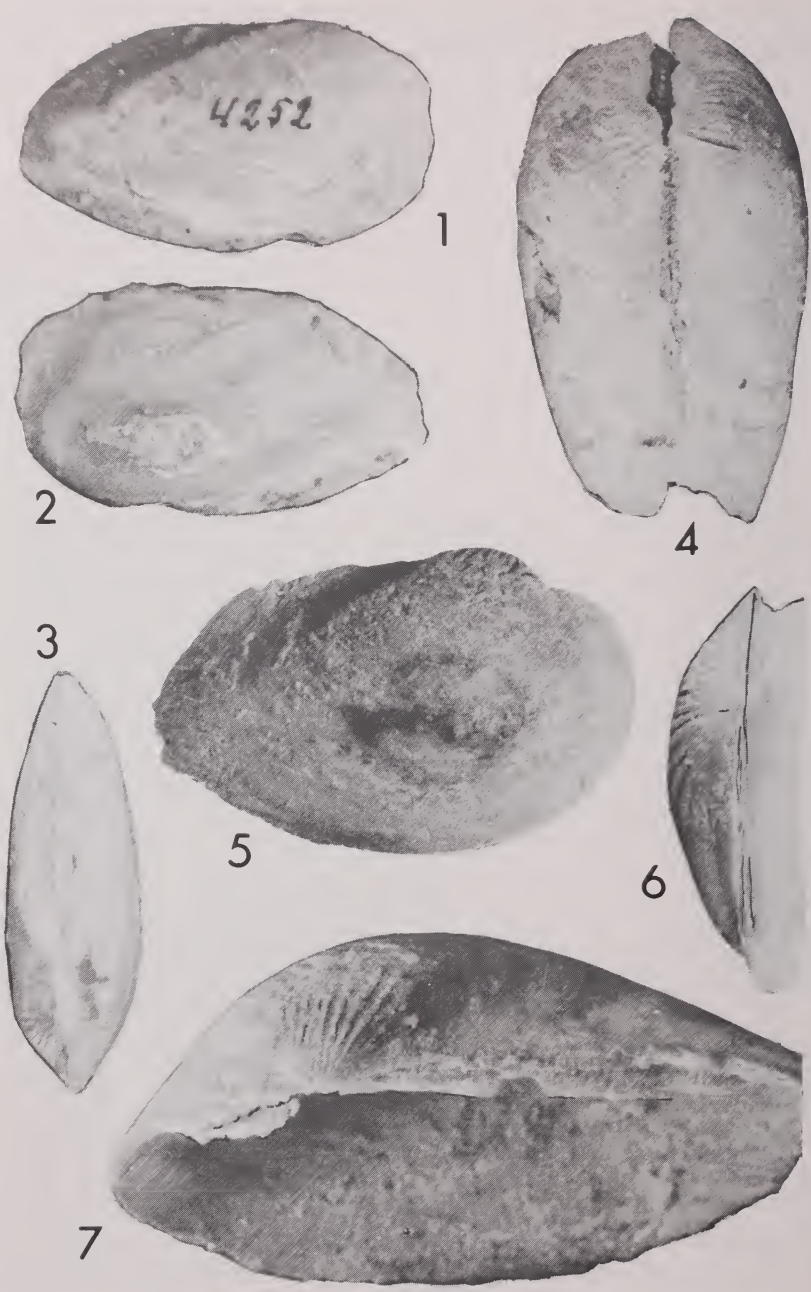
Parodiz, 1963: 145, pl. 11, fig. 1-4.

DESCRIPTION: Shell subelliptical, rounded in front and narrowed posteriorly. Umbo placed at the middle of the anterior slope, not prominent and radially striated. Dorsal margin straight in its distal part, forming a 60° angle with the anterior side. Posterior ridge scarcely noticeable. Concentric lines of growth regularly spaced (about one-half mm. apart) on the upper portion of the shell, and more conspicuous at the center, where they are stronger, waving, and interrupted by groove-like depressions, giving to the surface a rugose, imbricate aspect similar to the living forms of the *chilensis-granosus* group. Dimensions, 66 mm. long, 41 mm. high, 10 mm. between valves. The height corresponds to 62% of the length.

TYPE LOCALITY: Paso Tinguiririca, between the headwaters of the rivers Tinguiririca and Grande, province of Colchagua, Chile, close to the bordering Argentine province of Mendoza. A single specimen collected by José N. Thomas in 1916, from strata representing a northwestern extension, or synchronical equivalent, of the Jahuel Formation, Paleocene. Type in CM.

The fossil has both valves strongly compressed and fractured under the umbo by diastrophic pressure, resulting in a very thin profile. In natural condition the shell probably had a convexity similar to *chilensis patagonicus.* Otherwise the specimen is remarkably well preserved. Contrasting with the coal-black surface, the wrinkles or grooves are filled with an oxidized substance (limonite) of rusty color.

Relationship of *transandinus* with the recent and sympatric *D. chilensis* are obvious, but the sculpture recalls more that of *D. granosus.* Although these two living species are geographically widely separated, they belong to a common stock with parasitic glochidia of *Diplodon, sensu stricto. D. transandinus* also resembles *Hyridella menziesi* from New Zealand, not only in the flatness of the shell, but in outline and surface as well. The affinites of certain South American species with others from Australia and New Zealand were well known but such


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knowledge was limited to living forms. *D. transandinus* establishes a new link as old as the early Tertiary.

Diplodon burckhardti (Mayer-Eymar)

Unio burckhardti Mayer-Eymar in Burckhardt, 1900:24, pl. 26, fig. 6-7.
Diplodon sp., Frenguelli, 1940:80.

DIAGNOSIS (translation): "Shell trapezoidal-oval, moderately inflated, inequilateral, irregularly rugose, umbo a little swollen. Anterior portion short; posterior elongated, oblique and compressed, truncated; inferior long, almost straight but a little sinuous. Cardinal tooth in left valve thick and subtriangular. Long. 60, alt. 43, diam. 24 mm.".

TYPE LOCALITY: From limestone of Valle de Paula, East of Arroyo Pacunto (left affluent of the Bío-Bío between Gayetul Lake and Lonquimay River). Collected by C. Burckhardt 1898 in strata of same age as those of Lonquimay, Chile. Location of type unknown.

The original figure shows very little of the external surface of the valve, but its shape is different from — more oval and larger than — other Tertiary species. Mayer-Eymar said that it resembles *Unio michaudi* from the European Eocene but that "it is difficult to admit that these species of fresh-water mussels were spread so far apart in both hemispheres." This *Diplodon*, with other fresh-water shells also was found, and in the same strata, with *Potamolithus*, *Chilina*, in Neuquén, Patagonia, at the base of the thick series of Tertiary tuffs. Its age is upper Paleocene or perhaps lowest Eocene (see Frenguelli, 1940).

Diplodon nordenskjoldi (Steinmann & Wilckens)

Plate 4, fig. 3

Anodonta nordenskjoldi Steinmann & Wilckens, 1908:35, text fig. 1 on p. 98.

The specimen collected by Nordenskjöld consists of two matched open valves attached to a rock, showing only the external surface. The length of the shell is twice the height, with very fine and regular concentric striae. The umbo is inflated but not prominent. However, as that portion of the shell was eroded, the structure is unknown. The umbo is

PLATE 2

1-3. *Diplodon pehuenchensis* Doello-Jurado. Type, x2.
4-7. *Diplodon bondenbenderi* Doello-Jurado. 7. Type, x2. 4, 5, 6. xl.

well advanced, 6/7 of the total length. Anterior and posterior margins are well rounded. The general shape is as in *D. chilensis* or *transandinus*, except for the inflated umbo and striation. The last character, however, may be only an individual peculiarity, as species of this group seldom show such perfectly regular striation.

Since the umbonal structure and the hinge are unknown, the generic position of *nordenskjoldi* was uncertain. But as *Anodontites* (which is the sense in the Steinmann & Wilkens reference "*Anodonta*") never has been known, fossil or living (and it is unlikely to be found), so far south, it rather classifies with *Diplodon*.

TYPE LOCALITY: Río Cóndor, south of Bahia Inútil and across from Dawson Island, Tierra del Fuego, Chile, from the upper strata of "Minas de Carbón." According to Feruglio (1950) those "mantos de carbón" containing the *Notophagus* flora (Note 25), are equivalent to the Navidadean, that is of Oligocene age. Type in NR.

Diplodon oponcitonis Pilsbry & Olsson

Plate 4. fig. 1-2

Diplodon (Rhipidodonta) oponcitonis Pilsbry & Olsson, 1935:17, pl. 4, fig. 1, 2, 2a.

DESCRIPTION: "The shell approaches a circular form but it is a little longer than high; compressed, moderately thick. The anterior end is rounded, the posterior obliquely, steeply truncate, a little produced at the post-basal extremity; basal margin moderately convex; dorsal margin well arched. The surface is marked with fine and coarse wrinkles of growth. Beaks eroded, showing no special sculpture. The hinge is rather strongly developed; cardinal teeth stout; laterals curved, contiguous and rather thin and sharp in the left valve, single and rather thin in the right" (Pilsbry & Olsson).

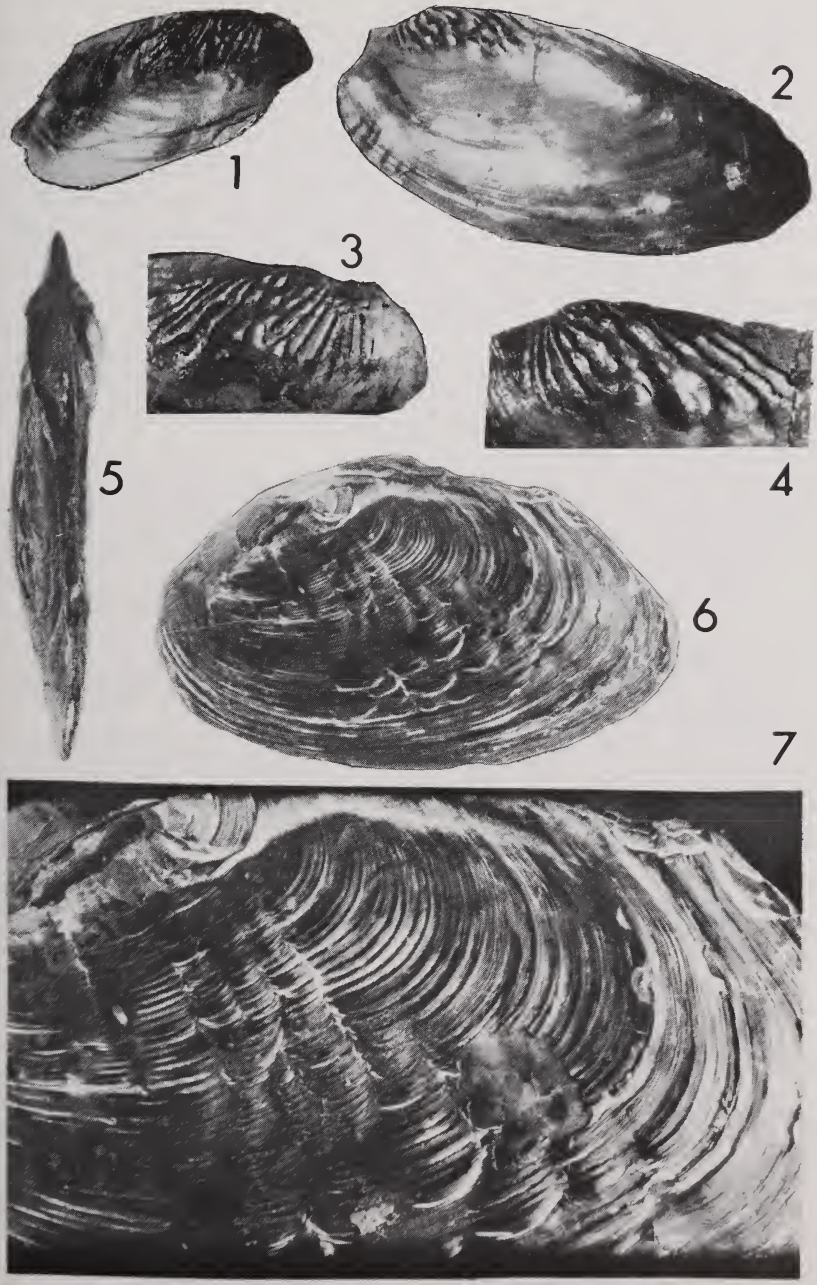
DIMENSIONS: Type: length, 43.5 mm., height, 37 mm. Paratype: length 43 mm., height, 35.5 mm. Type in ANSP.

TYPE LOCALITY: Oponcito River, affluent of the Magdalena, near Guanabanas, Colombia, from La Cira formation, upper Oligocene.

Its authors indicated that the general outline is as convex as in *Diplodon rotundus* (Wagner), a species typical of the San Francisco River in eastern Brazil, and belonging to the group *paranensis-variabilis*, usually placed in "*Cyclomya*" (=*Rhipidodonta*). Therefore the subgeneric denomination by Pilsbry & Olsson is correct. When

PLATE 3

1-4. *Diplodon gardnerae* (Marshall). 2. Type, x1.
5-7. *Diplodon transandinus* Parodiz. 5, 6, 7. Type. 5, 6., x1; 7., x2¼.


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compared with specimens of the living *D. paranensis* from the Paraná Basin, there are extraordinary similarities in flatness, in the dorsal subalate margin with undulations, posterior dorsal sulcus and ridge, and in marks of growth and hinge.

Diplodon oponcitonis, and the following species *latouri*, are from the same type locality and strata, and represent the two aspects of the subgenus *Rhipidodonta*: the flat and rounded (*oponcitonis*), which agrees better with the type of that subgenus, and the smaller, inflated, and stronger V-shaped sculpture of the *D. guaranianus* group. It is important to note that *D. rotundus* has a prodisoconch with sculpture of *guaranianus* type, and that the young shells are more elongated but somewhat alate, subsequently developing into a rounded and flat shape.

Diplodon latouri (Pilsbry & Olsson)

Plate 4, figs. 7-8

Triplodon latouri Pilsbry & Olsson, 1935:16, pl. 15, fig. 3-5.

The shells are small (18.5-24 mm. x 14.6-19 mm.) with very distinct chevron-like sculpture very similar to that of the living *guaranianus*. The enlarged figures in Pilsbry & Olsson, 1935, evidently are from young individuals, showing a perfect striation occupying the upper half of the shell, down to the central line, where it is abruptly interrupted. In other individuals the radial costulae are broken or tuberculiform, which are also characteristics linking *latouri* with *guaranianus*. The doubts entertained by the authors regarding the generic position were well justified "possible both are — *latouri* and *Hyria wheatleyi* with which was compared — referable to *Ecuadorea*." The hinge is unknown, but the outline of *latouri* is not aviculated as in typical *Triplodon*.

TYPE LOCALITY: Near Guanabanas and beds of Oponcito River, in the Magdalena Valley, Colombia, at the base of La Cira formation, Oligocene. Type in ANSP.

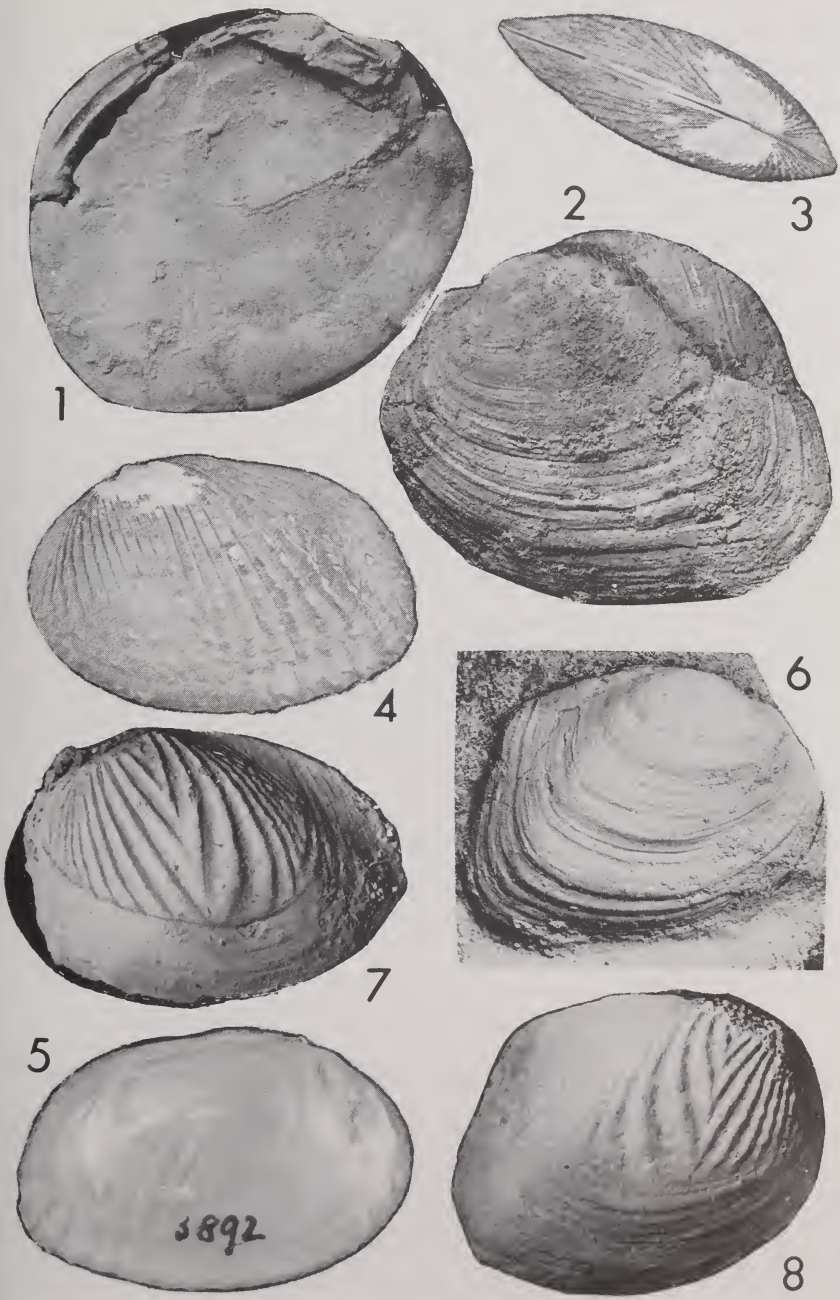
Diplodon chilensis patagonicus (d'Orbigny)

Plate 5, figs. 1-4

Unio patagonica d'Orbigny, 1835 No. 17; 1842 (Mollusques): 610, pl. 70, fig. 4.

PLATE 4

1,2. *Diplodon oponcitonis* Pilsbry. Type, x1.
3-5. *Diplodon pazi* (Hidalgo). Type, x2.
6. *Monocondylaea marshalliana* Pilsbry & Olsson. Type, x1.
7,8. *Diplodon latouri* (Pilsbry & Olsson). 7. Type, x2; 8., x2.


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Unio frenzelli Ihering, 1893:3, pl. 4, fig. 12.
Diplodon haupensis Bartsch, 1906:394, pl: 18, fig. 3, and 19, fig. 3. (*anapensis !* in Nautilus 20:36).
Diplodon patagonicus Ihering, 1907b:468.
Diplodon chilensis patagonicus F. Haas, 1930:180

The living specimens of *patagonicus* differ from *chilensis chilensis* by the marked rugose surface, deeper concentric lines of growth, and brownish-black (instead of olive-green) periostracum. The typical *chilensis,* however, offers such extremes in its range of variations in surface, shape, and hinge, that the separation of these forms into several species was based more on allopatry than on permanent phenotypical characteristics. The synonymy of *chilensis-patagonicus* is numerous, and it is found complete in F. Haas 1930. Describing *patagonicus,* d'Orbigny did not compare it with *chilensis.* Considering fossil forms, *chilensis patagonicus* has many characters in common with *transandinus,* and it is likely that during the Tertiary these forms covered a continuous and densely populated eastern area.

The type locality of *patagonicus* is "Río Negro," and it is found in abundance on the headwaters of that river, the Limay River, and in the Andean lake region of northern Patagonia, especially at Nahuel Huapi Lake. Fossils are better known from the western side.

Fossils from Esquel, western Chubut (collected by A. Tapia 1919), which I identified as *patagonicus,* are from the Valley of the Percey River (Colonia 16 de Octubre) which is the locality and the strata from which the fossils mentioned by Ihering (1907b) as "Rio Perrey" were taken. The matrix is a gray sandstone (Plate 11, fig. 4), forming "a continuous level with abundant remains of *Diplodon*" (Guiñazu 1940:30), which according to Feruglio (1949) is of Oligocene age. Southeast of Cerro Bagual, at "Pampa de Nahuel Huapi," Feruglio in 1926 collected inner casts of this *Diplodon* from sandy tuffs bearing the characteristic *Notophagus* flora in the so-called "Terciario carbonifero," equivalent to the base of the Magellanian Beds of the Oligocene (Note 25).

Diplodon chilensis and *transandinus* represented an old stock which survived in *patagonicus and granosus,* the latter of northern distribution. Geographically, the group is closer to that of *D. rhuacoicus,* although the route of that expansion is not well known. The group

PLATE 5

1-4. *Diplodon chilensis patagonicus* (d'Orbigny). Specimens from living populations, x1.


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is also linked to the New Zealand Hyriidae, probably by expansion through Antarctica, which in the early Cenozoic had a benign climate. This hypothesis has been supported by many authors since Darwin.

All the fossil specimens of *chilensis patagonicus* mentioned above are relatively smaller than the living populations. (Type in BMNH.)

Diplodon liddlei Palmer

Plate 8, figs. 1, 4

Palmer, 1941:404, pl. 8, fig. 1-5.

ORIGINAL DESCRIPTION: "Shell elongated-quadrate, plump, anterior end short, posterior end flaring dorsally with a narrow wing above the hinge line; posterior dorsal area concave, sloping ventrally; hinge with two psuedocardinals in the right valve, the lower tooth the larger, with a large socket between; correspondingly a large pseudocardinal in the left valve; anterior adductor and retractor muscle scars preserved on paratype; umbones ornamented with radial ribs of short interlocking V-shaped pattern. The lower portion of the shell is sculptured with coarse lines of growth only. Length 35 mm., height 28 mm., semidiameter 6 mm.".

TYPE LOCALITY: Center of Azogues anticline, 3 kms. N.W. of town of Azogues, province of Canar, Ecuador, coll. R.A. Liddle, 1940. Miocene. Type in PRI.

This species differs from *D. guaranianus biblianus* by its more rounded shell but principally by the hinge. Ornamentation appears to be different too, but as this character is very variable in species of the group, it is less obvious. The position and shape of the hinge is, according to Palmer, closer to that of *mogymirin* Ortmann, that is a *Diplodon sensu stricto,* not a *Rhipidodonta* as *biblianus. D. mogymirin* is, according to F. Haas, Bonetto, and my own observations a form to be included within the variations of *D. expansus. D. liddlei* as belonging to the *guaranianus* group is a *Rhipidodonta.* In shape it may be compared with *D. rothi,* another Miocene species, but the latter lived far to the south, its sculpture is inconspicuous, and it is very rare.

Diplodon guaranianus biblianus (Marshall & Bowles)

Plate 6, figs. 1-7
Plate 8, fig. 6

Ecuadorea bibliana Marshall & Bowles, 1932:5, pl. 1, fig. 7-8. Palmer, 1941:401, pl. 7, fig. 1-6. Modell, 1950:143.

Castalioides laddi Marshall, 1934:78, fig. 1-4. Palmer, 1941:402, pl. 8, fig. 6-8.

Ecuadorea laddi, Modell, 1950:143.

ORIGINAL DESCRIPTION: "Shell rather compressed, subelliptic, slightly narrower in front. Concentric sculpture of fine growth striae, with few of the rest periods a little accentuated. Radial sculpture of a number of riblets as to form a series of V's, each nesting into the succeeding one, and with other riblets at the front and back which if continued would form additional V's. The anterior prong of each V is narrow, clear-cut, and nearly straight. The posterior prong is heavier and more irregular and curves toward the front end of the shell. At the lower end where the radial sculpture dies out, the surface is somewhat pimpled. The posterior dorsal area with several (five or six) distinct flutings running across it to the margin. The dorsal and ventral margins both arquate. L. approx. 33 mm., H. 24, diam. (half) 11 mm.".

TYPE LOCALITY: Biblian, few miles N.E. of Azogues and S.W. of Canar, Ecuador, found in strata of lower Miocene. Type in USNM.

Marshall remarked that in sculpture, *bibliana* closely resembles *Castalia pazi* Hidalgo [from Imbabura River in northern Ecuador], a living species "which does not have the flutings of the posterior dorsal area." Such character has little, if any, specific value because several species of *Diplodon* in this and other groups present it in different degrees of development. Although a comparison of *D. biblianus* and *D. pazi* reveals similarities, Marshall's species is closer to *guaranianus* in form and sculpture. On the other hand, excellent photographs of the syntype of *pazi* (received by courtesy of Dr. Zilch, of the Senckenberg Museum), show clearly the differences between *pazi* (Plate 4, figs. 3-5) and *guaranianus*. The first has a weaker cardinal tooth; the ribs are marked on the interior of the shell, with more iridescent nacre; and the posterior adductor is very shallow (not conspicuous and deep as in *guaranianus*). All these characters place *pazi* in closer relationship to *hylaeus*. The sculpture of this last species, however, does not reach the lower margin as in *pazi*. The three species can be satisfactorily separated as follows:

1. Strong, more angulated shells		*guaranianus*	
2. Slender, more ovate shells	*pazi*		*hylaeus*
3. Interior pearly white		*guaranianus*	
4. Interior bluish, iridescent	*pazi*		*hylaeus*
5. Sculpture reaching lower margin	*pazi*		
6. Sculpture down only to middle		*guaranianus*	*hylaeus*
7. Ribs visible from interior	*pazi*		*hylaeus*
8. Muscle scar strong, deep		*guaranianus*	
9. Muscle scar shallow, weak	*pazi*		*hylaeus*
10. Cardinal tooth large, strong		*guaranianus*	

11. Cardinal tooth small, weak	*pazi*	*hylaeus*
12. Southeastern distribution (Parana-Paraguay)	*guaranianus*	
13. Distribution in mountain streams of Bolivia		*hylaeus*
14. Distribution in northwestern Ecuador	*pazi*	

The only important similarity between *guaranianus* and *hylaeus* occurs at No. 6, while *pazi* and *hylaeus* coincide in 2, 4, 7, 9, and 11, but differ in 5 and 14. Whether *pazi* should be subordinated as a subspecies of *hylaeus* has to be decided on the basis of substantial populations of both type localities, but at present there is no such evidence.

Diplodon guaranianus biblianus shows a considerable degree of variability, judging from the specimens figured by Palmer from the type locality (Plate 8, fig. 6). The hinge differences between *biblianus* and *laddi* (Plate 6. figs 1, 4, 5) are the same as those I have seen in series of living *guaranianus,* for which the character does not justify any generic or subgeneric separation. Modell (1950:143) has already recalled the sculptural similarities of *Castalioides laddi* and *D. guaranianus* as being the same as in *Ecuadorea.*

All these and related species were usually referred in the literature as belonging to the "*Diplodon hylaeus* group," but d'Orbigny, when describing this species, said that it was very rare, living in stony streams (type locality, Palometas River, affluent of the Piray, in Santa Cruz de La Sierra, Bolivia). Afterwards the species was recognized by Ortmann (1921:473) from a single specimen from about 400 miles east of the type locality, on the Paraguay River, which does not agree completely with d'Orbigny's illustration. In addition, F. Haas, the only author who revised the syntypes of *hylaeus,* regarded it as different from *guaranianus.* I assume that all other specimens collected in eastern localities, mentioned by authors as *hylaeus,* and those I collected from the Paraná, belong to *guaranianus.* Until new collections are made in the streams of upper Bolivia, the variations and relationships of *hylaeus* remain doubtful. On this account I am referring to the "*guaranianus-group,*" as this is the better known species (Note 38). It is obvious that Modell's arrangement within *Ecuadorea* corresponds to the same group. The following table summarizes the systems of Modell, Ortmann, F. Haas, and Bonetto:

TABLE 4. DIPLODON GROUPS

Ortmann 1921	F. Haas 1930	Modell 1950	Bonetto 1961b
D.hylaeus group:	*D.hylaeus* group:	*Ecuadorea* + *Castalioides:*	*Rhipidodonta:*
No fossils mentioned	No fossils mentioned	*E.laddi* *E.bibliana*	No fossils mentioned
D.hylaeus	*D.hylaeus*	*E.hylaea*	*D.hylaeus* group
D.guaranianus	*D.guaranianus*	*E.hylaea guaraniana*	*D.hylaeus guaranianus*
	D.guaranianus fluctiger	*E.fluctiger*	
	D.guaranianus pazi	*E.pazi*	*D.hylaeus pazi*
		Schleschiella:	
D.hasemani	*D.guaranianus hasemani*	*S.iheringi hasemani*	*D.hylaeus hasemani*
		S.asuncionis	*D.hylaeus asuncionis*
lateolus-burroughianus group	*D.burroughianus*	*S.burroughianus*	*D.variabilis* group
	D.asuncionis		
	D.wheatleyanus	*S.wheatleyanus*	
D.charruanus group	*D.charruanus* group	*S.rhuacoica*	
D.parallelipipedon	*D.parallelipipedon* group	*S.parallelipipedon*	*Diplodon, sensu stricto*

Diplodon rothi Ihering

Plate 7, fig. 4

Ihering, 1904:232; fig. 6; 1907 b:466.

DESCRIPTION: The valves are compressed and thin, with umbos very close to the anterior margin, deeply striated radially with grooves clearly separated. The

radiations converge at the center into a V-shaped pattern. Small in size: 30 mm. long, 21 mm. high, 11 mm. between valves. From these characteristics of the type, which was embedded in the matrix (hinge unknown), it is deduced that the fossil corresponds to an immature specimen, although the differences are remarkable, as Ihering said, from other known *Diplodon*.

TYPE LOCALITY: Arroyo Lele — or Leleque — at the foot of Sierra Leleque, halfway between Ñorquincó and Esquel, on national route 40, western Chubut, Patagonia. Also found at the nearby locality of Arroyo Lepa. Both collected by S. Roth (1897 or 1898). This collecting data agrees with the label, although Ihering in his catalogue of 1914 indicated Hauthal as the collector. From fine yellowish tuffy sandstone which Feruglio (1949) recognized as the Colloncura Beds (= Friasean formation of Kraglievich, Feruglio and Simpson), accepted by most authors as middle Miocene (Note 25). Type in MACN.

Diplodon gardnerae (Marshall)

Plate 3, figs. 1-4

Eodiplodon gardnerae Marshall, 1928:4 pl. 1, figs. 2, 8.
Eodiplodon pebasensis Marshall, 1928:5, pl. 1, figs. 5-7.

Diplodon gardnerae and *pebasensis* are both from the same type locality and strata: Pebas, Iquitos region, Peru, from the Pebas formation, upper Pliocene, collected by J. T. Singewald. (Type in USNM.)

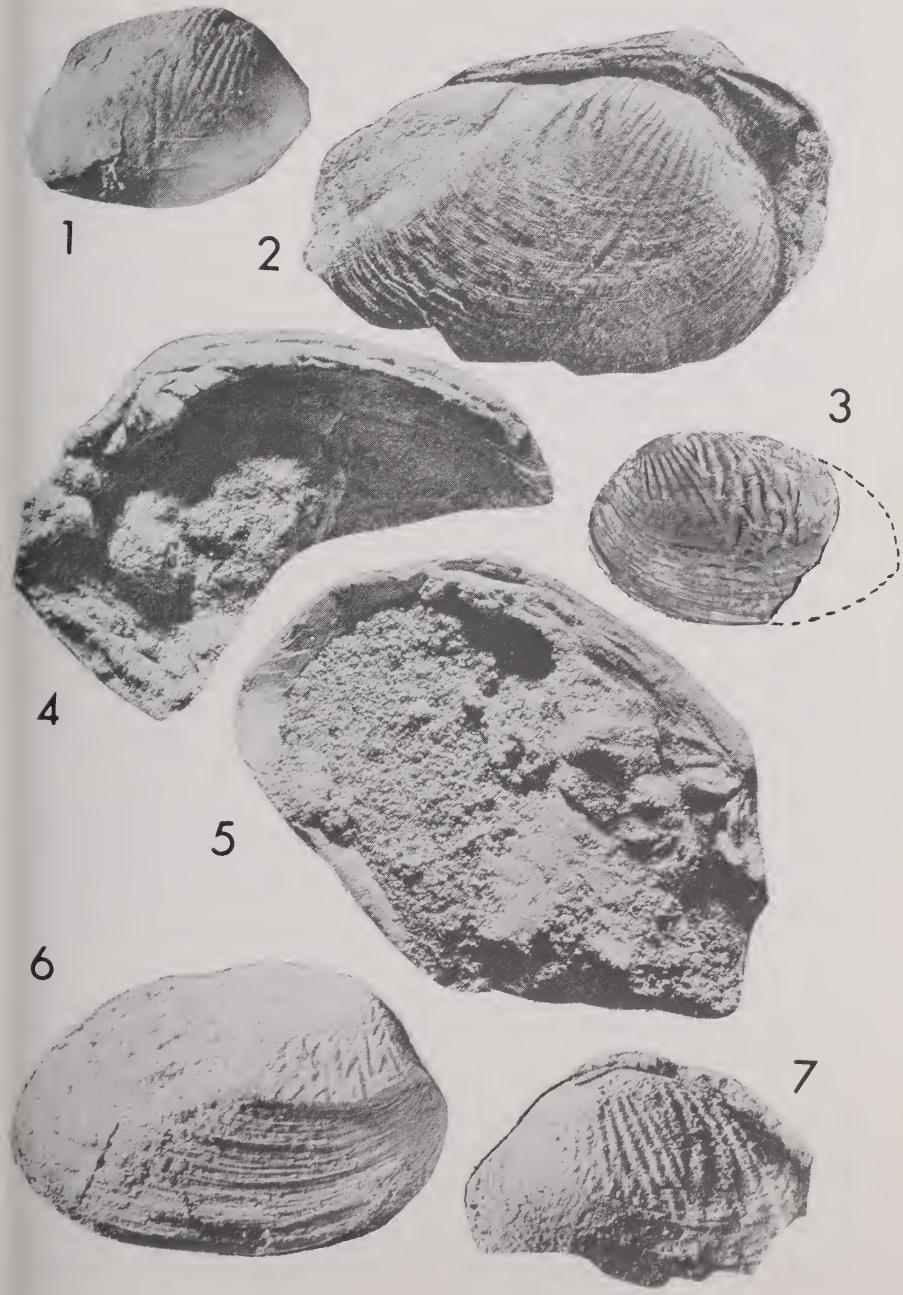
Most of the characteristics diagnosed by Marshall for *pebasensis* can be included among those of *gardnerae*, which are summarized as follows:

Dorsal margin arched or nearly straight posterior to the umbo, and anterior to it descends rapidly. Ventral margin regular and broadly curved, rounding into the anterior. On the posterior portion the shell is narrower, with well marked ridge. At the anterior part of ventral margin there are five radiating threads. Umbonal sculpture consists of granular, V-shaped riblets. The posterior side has another four or more radiating threads. Surface rather smooth. Adductor scars well marked but not deep. Pallial line about 6 mm. wide. Length (for *gardnerae*) is 64 mm., height 30 mm., diam. with both valves 16 mm., *pebasensis* 25 mm. x 13 mm.

D. pebasensis is just a small, broken specimen of *gardnerae* with a very slight difference in shape, and the distance from the umbo to anterior edge in both forms differs by only 2 mm. Also the "apparently rather compressed" (Marshall) form of *pebasensis* is probably due to diastrophic pressure, as we have seen in other species of fossil *Diplodon*. The umbonal sculpture is the same in both and, if in

PLATE 6

1,4,5. *Castalioides laddi* Palmer = *D. g. biblianus*. 1. Type, x1; 4., x2; 5., x1½.
2,3,6,7. *Diplodon guaranianus biblianus* (Marshall). 2. Type, x1¾; 3., x2; 6., x1.


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pebasensis it descends more conspicuously, it is just what is to be expected in relatively young individuals. The same sculpture is shown in the living *ellipticus* from Brazil (see F. Haas 1931, fig. 28 as *D. granosus multistriatus*), and on this feature alone, the maintenance of a different genus, *Eodiplodon,* is superfluous.

Diplodon singewaldi (Marshall)

Plate 7, figs. 1-3

Prodiplodon singewaldi Marshall, 1928:2, pl. 1, figs. 3, 6.
Prodiplodon paucarpatensis Marshall, 1928:4, pl. 1, figs. 2, 8.

COMBINED DESCRIPTION (characters of *paucarpatensis* between brackets): "Shell compressed [rather compressed], somewhat quadrate [trapezoidal], rounded in front [slightly narrower], slopingly truncated at the rear. Dorsal margin arches, making a broad, scarcely noticeable, angle with the posterior margin [nearly straight, rounding into the anterior]. Ventral margin little curved at the median portion, rounding into the anterior, making a broad angle with the posterior. Beaks forward, 19 mm. behind the anterior end [18 mm.], 51 mm. from the posterior [56 mm.]. Posterior ridge low, slightly angulated [rounded]. Sculpture of prominent [well marked] concentric lines [the whole shell lacks its outer surface and is nearly white]. Umbonal area sharply and closely sculptured with radiating threads or riblets [similar to that of *singewaldi*]; at the anterior portion narrow, curved, somewhat granulous; posteriorly increasing rapidly in size; the middle portion V-shaped. The sculpture shows tendency to continue beyond the umbonal area. Pseudocardinal plate-like, nearly parallel to dorsal margin; lateral tooth long and curved. Related to *paucarpatensis* [but differing in form]. Length 70 mm., height 39 mm., diameter if both valves were present about 20 mm. [74 mm., 39 mm., 18 mm.]

The minor differences between *singewaldi* and *paucarpatensis* have no specific value. As to the genus *Prodiplodon,* the given characteristics were "several V-shaped undulations" — not very different from *Eodiplodon or Ecuadorea* — which also are present with many degrees of variations in living species of *Diplodon* (Note 26).

TYPE LOCALITY (of both *singewaldi* and *paucarpatensis*): Paucarpata, on the Marañon River N.W. Peru, Upper Pliocene strata probably of the Pebas Formation. Type in USNM.

Diplodon bassleri (Marshall)

Plate 7, fig. 6

Prodiplodon bassleri Marshall, 1928:3, pl. 1, fig. 1.

The original description of *bassleri* closely approaches except for minor details, that of *singewaldi.* The characteristics of the umbonal

sculpture were emphasized, indicating that the V-shaped pattern point "in the general direction of the postero-ventral margin while in *singewaldi* they are directed toward the point anterior to the middle of the ventral margin." Such distinction is caused by the most advanced position of the umbo, and the low, rounded ridge departing from it, running almost parallel to the dorsal margin and ending higher than in *singewaldi*. This makes a difference between the two species of greater value than the elliptic outline in Marshall's sense. Both are very close in size: length 60 mm., height, 38 mm., diameter (estimating both valves) 16 mm. (Type in USNM.)

D. bassleri was collected at Pebas, Peru, by Harvey Bassler. Of the five species described by Marshall from the same region, *bassleri* seems to differ more conspicuously, so far as the type is concerned.

Diplodon diluvii (d'Orbigny)
Plate 9, fig. 2

Unio diluvii d'Orbigny, 1842, 4: 127, pl. 7, figs. 12, 13.
Diplodon diluvii, Ihering, 1907b: 467.

Although D'Orbigny based his description on inner casts, some remains of the shell also were observable since he referred to the surface as being smooth, and gave the following principal characteristics: umbonal portion deep (inside) and advanced, posterior margin elongated and arched above, obliquely truncated below, muscle areas trilobed, large and deep. The author also compared *D. diluvii* with *D. patagonicus*, from which *D. diluvii* was distinguished mainly by its truncated posterior margin. It also bears resemblance to *colhuapiensis* of the Paleocene, and before describing this species, Ihering labeled his specimens from Colhue Huapi as *diluvii* (Note 24). But *D. diluvii* differs clearly from these two species mentioned by its shorter and swollen form, with well-marked posterior ridge, but especially by its considerably thicker ventral-anterior margin, which in some specimens, amounts to 7 mm. Inner plaster casts of *D. patagonicus*, for comparison, show these differences conspicuously.

Although geologists have referred it to the fresh-water strata of the Entrerrian (= Rionegran, d'Orbigny "grès à Unio") with abundant "unios," the species is very rare in collections. Dr. C. P. Nuttall of the British Museum (N.H.) informed me that the type cannot be found in that museum collection where the other d'Orbigny materials are preserved, and it is probably lost. From the only lot at my disposal,

consisting of four single valves (two inner casts and fragments), I selected as neotype (plate 9, fig. 2) a right valve, relatively well preserved, collected by R. Wichmann in 1924 on the right bank of the Colorado River (at Colorado), province of the Río Negro, Argentina. The original locality was "Falaises du Nord" (Barrancas al Norte) of the Negro River, less than 100 miles south of the selected neotype locality (farther west the rivers Negro and Colorado become closer). The age of the deposits is lower Pliocene (Note 20). The neotype is in CM.

Diplodon diluvii does not belong to the group of older, Paleocene species (as *D. colhuapiensis, D. patagonicus*). Rather it should be included in the *Diplodon delodontus* complex. In fact, the shape, hinge, thickness, and muscle scars are similar to some forms considered subspecific *delodontus (uruguayensis, wymani)* and also to *D. beskeanus* (Note 40).

DIMENSIONS (IN MM.)

Length	Height	Half-diameter	Diameter
50	29	10 (d'Orbigny)	—
50	42	—	—
55	39	—	—
62	40	—	15 (neotype)
64	42	—	—

The height of the shells is very variable in the four valves at hand, ranging from 64 per cent to 84 per cent of the length, always higher than *D. patagonicus,* in which this proportion is no more than 52 per cent.

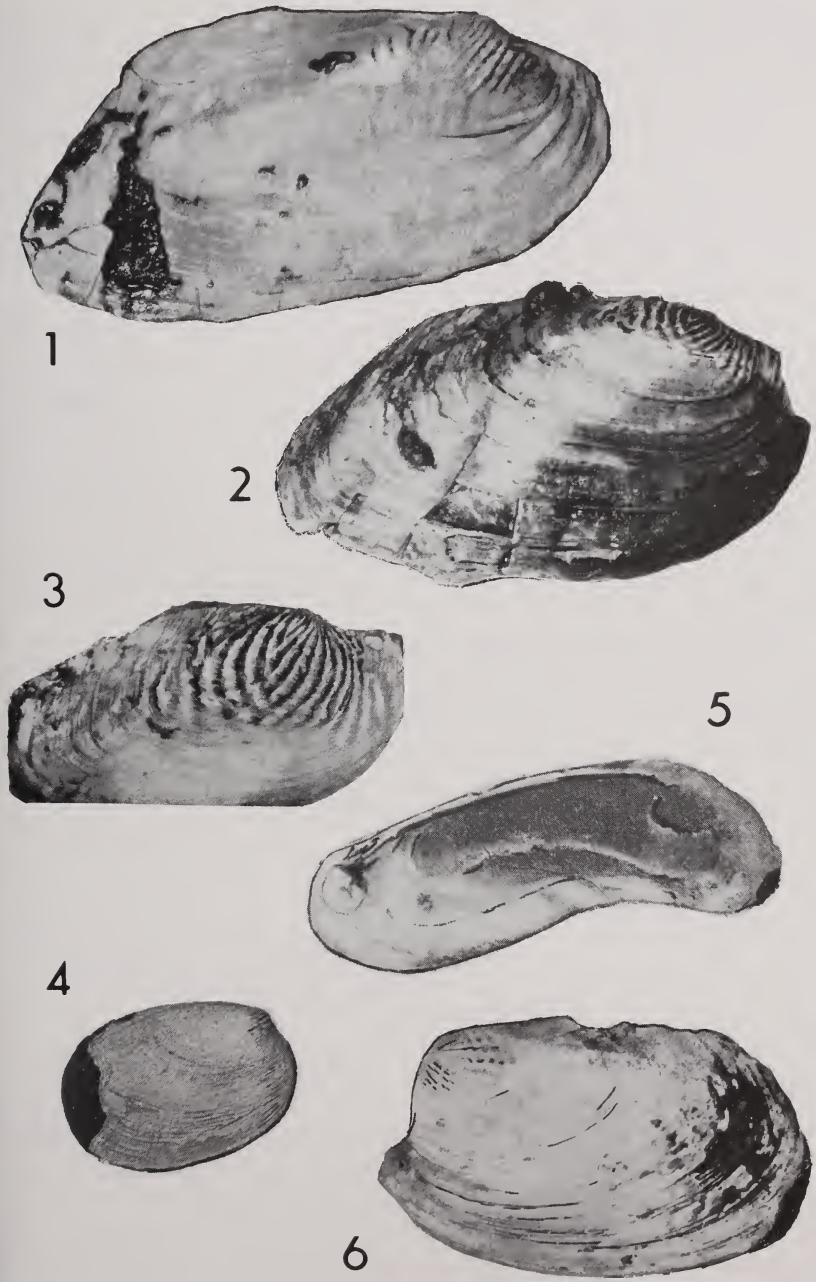
Diplodon fraus Ihering

Plate 7, fig. 5

Modiola contorta Borchert, 1901:27, pl. 2, fig. 3, 4.
Unio contortus, Ameghino, 1906:517, (not *Unio contortus* Huede = *Arconaia lanceolata* Lea from China).
Diplodon fraus Ihering, 1907b: pl. 18, fig. 129. Frenguelli 1920:127.

PLATE 7

1-3. *Diplodon singewaldi* (Marshall). 2. Type, x1; 1., x1; 3., x2.
4. *Diplodon rothi* Ihering. Type, x1.
5. *Diplodon fraus* Ihering. Type, x1.
6. *Diplodon bassleri* (Marshall). Type, slightly reduced.


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The specimen described by Borchert in 1901 was collected some forty years before by A. Bravard at Paraná, Entre Ríos, in sediments which according to Frenguelli belong to the Pliocene. But the later author also had doubts that the specimens were found "in situ" because of the probability of mixture, caused by the falling and drifting of rocks, which often occurred at the Paraná Ravines (Note 27). Ihering's figure of 1907b of *fraus* bears extraordinary resemblance to *Diplodon parallelipipedon*, as if it were abnormally distorted by adaptation to hard substratum (a condition not uncommon in other freshwater species (as *Anodontites tenebricosus*). I did not find specimens of *fraus* when I revised Ihering's collection in the Argentine Museum of Natural Sciences, and it is not listed in the author's catalogue of 1914. Apparently the species was based only on Borchert's description. Frenguelli (1920) did not find the species at Paraná, and the only specimen he saw with adhered portion of matrix (because of which he identified the structure with the sediments of level No. 7 of his Tertiary sequence at Paraná) was given to him by Doello-Jurado.

Diplodon fraus is a small species among its relatives, if the natural size indicated in the illustration is correct: length 62 mm., height 20 mm.

The characteristics indicated by Ihering are essentially a description of the hinge, which is within the variations of *Diplodon parallelipipedon*. New and better materials will be needed to determine whether *fraus* is merely an extinct form or a variation of that species.

Tribe Prisodontini

Genus *Paxyodon* Schumacher 1817

= ? *Triquetra* Klein

Type: *Paxyodon ponderosus* Schumacher
= *Mya syrmatophora* Gronovius

Paxyodon priscus (Ihering)

Pleiodon priscus Ihering, 1912:489.

This species was described from an incomplete valve found by J. Pacheco, of the Geographical Commission of São Paulo, at Itaimbe, Municipio Taquiritinga, São Paulo, Brazil. It shows a taxodont-like hinge similar to that of *Paxyodon ponderosus* Schumacher, as in this group the tendency is to develop pseudotaxodont hinges formed by parallel protuberances. The fragmentary shell does not show the semi-

alate dorsal line of *ponderosus,* but probably it was similarly winged.

The age of the fossil was not originally indicated. Oliveira & Leonardos (1943:606) assumed that it belongs to the Bauru formation in "strata with dinosaurs." I suspect that in the history of these strata there prevails the same confusion created for the "strata with dinosaurs" of Patagonia. It belongs rather to the upper section, "Arenito Bauru" which overlies the "basal Bauru conglomerate." Also known from the same stage is a Chelonian, *Podocnemis brasiliensis* Staesche, a genus also found in the "Puca" (upper section) Santabarbaran of northern Argentina (Note 28). For its position and correlations the Arenito Bauru should be considered Paleocene.

Ihering emphasized the importance of this *"Pleiodon" (= Iridina)* as an argument in favor of his thesis of African (Archaehelenic) faunistic elements in Brazil, but *Paxyodon,* belonging to the Hyriidae, is not Gondwanic. It is not listed in Ihering's catalogue of 1914, and the location of the type is unknown (probably MP).

Genus *Triplodon* Spix, 1827

Type: *Triplodon rugosum* Spix
= *Hyria corrugatta* Lamarck

?*Triplodon longula* Conrad

Triquetra-Hyria-longula Conrad, 1874:29, pl. 1, fig. 10.
Hyria sp., de Greve, 1938: 20, pl. 7, figs. 24-25.

Of this species no more is known than its original description:

"Subrhomboidal, slightly ventricose, elongated, *scarcely alated,* hinge and ventral margin near parallel; anterior margin slightly emarginate; dorsal line convex, ventral margin nearly straight; umbonal slope rounded except on the umbo where it is subangular; umbo flattened, with longitudinal and transverse zigzag plications; posterior margin obliquely truncated; cardinal teeth of right valve four, the anterior one elongated and compressed, rectilinear, two diverging teeth immediately under the apex, and a much less elevated linear oblique tooth between the two anterior teeth; in the left valve two very oblique diverging teeth anterior to the beak, and two or three very small direct teeth under the beak." (Emphasis mine.)

Under the name "*T. longula* (young) Conrad," the same author (1874:30, pl. 1, fig. 13) refers to a fragment of shell, different from the preceding description of *longula,* which I think is a specimen of the living *T. rugosum* (location of type unknown).

Both valves were from the "Upper Amazon at Pebas" (Peru), but it is not certain that they belong to the typical Pliocene Pebas formation. If they do, they must be from the uppermost section.

Superfamily MUTELACEA
Family MYCETOPODIDAE Gray, 1840
(restricted Conrad, 1853)
Subfamily MONOCONDYLAEINAE Modell, 1942
Tribe Monocondylaeini
Genus *Monocondylaea* d'Orbigny, 1835

Type: *M. paraguayana* d'Orbigny

= *Aplodon Spix*, 1827 (not
Rafinesque, 1818)
Spixiconcha Pilsbry, 1893

The shells of the Monocondylaeini are small with rare exceptions, thick, rather gaping, and have a wide prismatic area. The hinge has one (occasionally two) tuberculiform tooth. The periostracum (in living species) is clothlike. Unfortunately these characters are not observable in the three fossil species listed below, described as *Monocondylaea* by their general rectangular-subquadrate form and lack of radial sculpture. The concentric striae of growth are stronger in *M. marshalliana* than in the other species of the genus (hinges unknown in the three species).

Monocondylaea marshalliana Pilsbry
Plate 4, fig. 6

Pilsbry, 1935:17, pl. 14, fig. 3.

Laciran age, (upper Oligocene) at Oponcitos River, near Guanabanas, Colombia. Type in ANSP.

Monocondylaea azoguensis Palmer
Plate 8, fig. 5

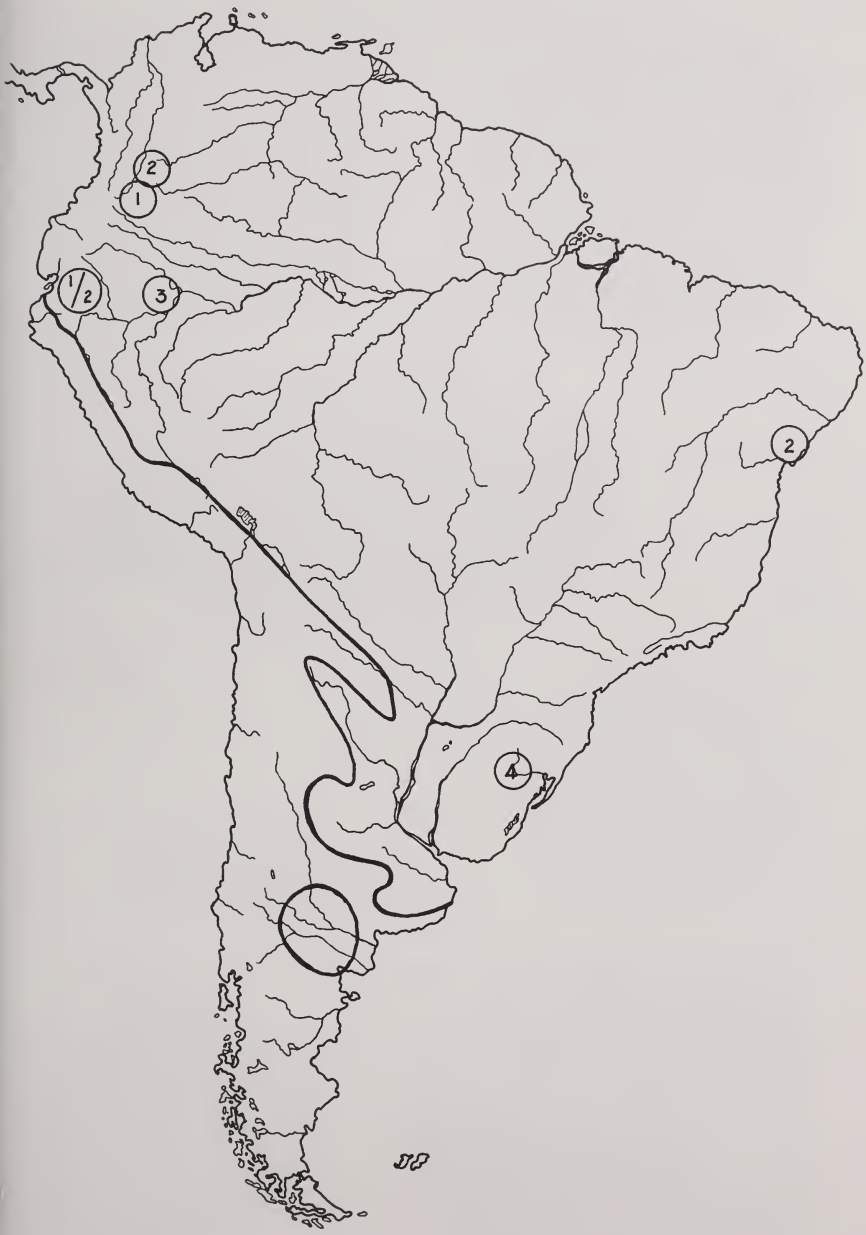
Palmer, 1941:405, pl. 9, fig. 8.

Biblian sandstone (lower Miocene), 3 km. N. of Azogues, Province Canar, Ecuador.



MAP 3

Heavy lines indicate western and southern distributional limits of living Mycetopodidae. Populations still exist in the encircled Patagonian area. Numbers indicate fossil localities: 1. *Monocondylaea*, Oligocene-Miocene; 2. *Anodontites*, Paleocene; 3. *Leila*, Pliocene; 4. *Fossula*, upper Tertiary.


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Monocondylaea pacchiana Palmer
Plate 8, figs. 2, 7

Palmer, 1941:405, pl. 9, figs. 1, 2.

Biblian sandstone at Quebrada Paccha, Ecuador. Both types in PRI.

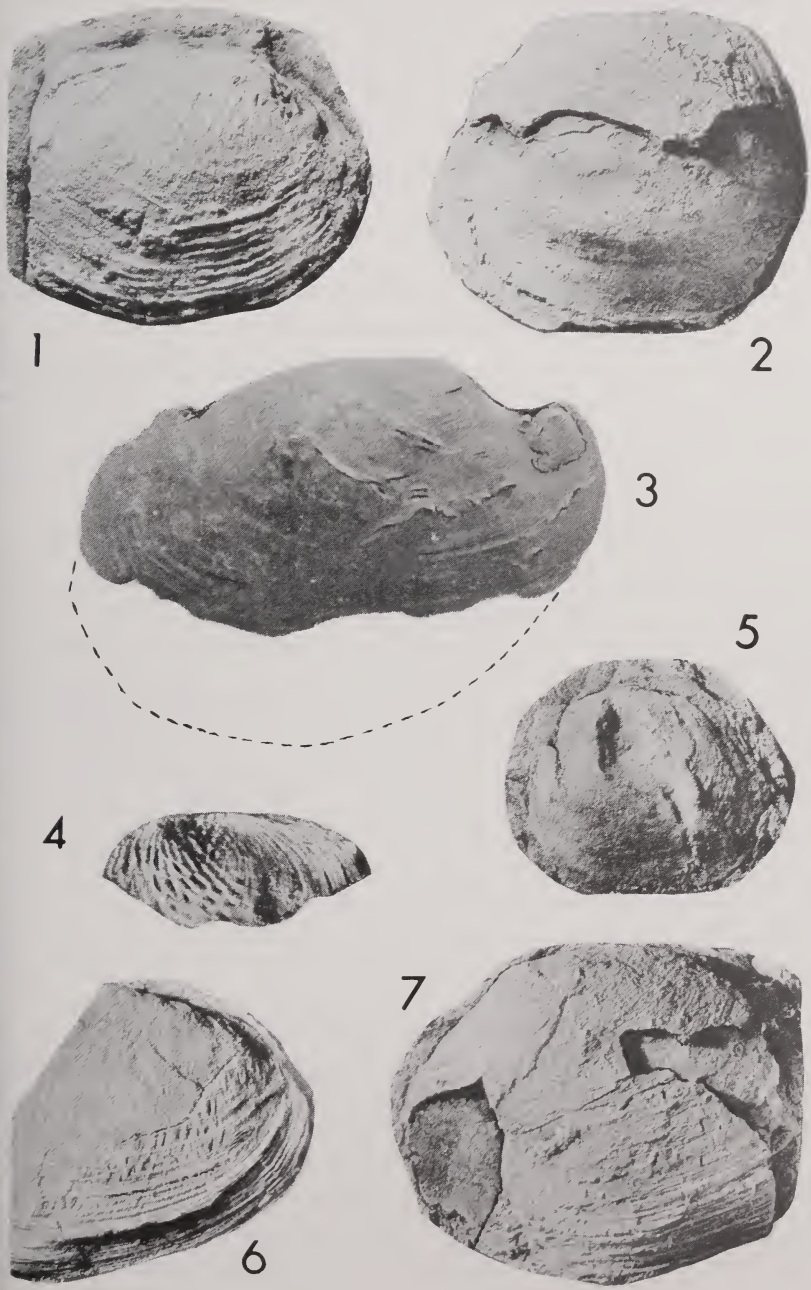
The summarized characteristics of these three species are compared in the following (Table 5):

TABLE 5. CHARACTERISTICS OF THREE SPECIES OF MONOCONDYLAEA

marshalliana	*azoguensis*	*pacchiana*
Shell short, trapezoidal	Short, quadrate	Rectangular, longer than *azoguensis*
Anterior end rounded	Rounded and not produced below beak	Sloping, short
Dorsal margin high, subalate	High	Straight, broad
Porterior end truncated, wider	With obscure fold	Oblique, rounded below
Basal margin moderately convex	Rounded	Convex on the sides, rather straight at the middle
Posterior ridge well marked	Obscure	Obscure
Sculpture coarse, concentric wrinkles	Smooth	Smooth
Hinge unknown	Unknown	Unknown
Length 33 mm.	29 mm.	40 mm.
Height 26 mm. (78% of length)	25 mm. (86% of length)	33 mm. (82.5% of length)
Half-diameter 7 mm. (20% of length)	5 mm. (16.6% of length)	10 mm. (25% of length)

PLATE 8

1,4. *Diplodon liddlei* Palmer. Type, x1.
2,7. *Monocondylaea pacchiana* Palmer. Type, x1.
3. *Fossula derbyi* (Ihering). Type, x1.
5. *Monocondylaea azoguensis* Palmer. Type, x1.
6. *Diplodon guaranianus biblianus* (Marshall). x1.


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M. marshalliana and *M. azoguensis* are approximately equal in diameter, and *pacchiana* is more compressed. *M. marshalliana* is the shortest and *azoguensis* the highest. *M. marshalliana* was indicated as similar to *parchappi,* but it compares more nearly with the form *franciscana* of *M. corrientesensis* d'Orbigny (Note 29). In shape *azoguensis* and *pacchiana* are closely related. Not knowing the interior of the shells and their hinges, however, the true relationships are still uncertain, inasmuch as in general shape they resemble *Haasica.*

Tribe Fossulini Bonetto, 1966
Genus *Fossula* Lea, 1870

Type: *Monocondylaea fossiculifera* d'Orbigny, 1835

Fossula derbyi (Ihering), 1907b
Plate 8, fig. 3

Diplodon colhuapiensis (in part) Ihering, 1903:217.
Diplodon derbyi Ihering, 1907b:466, pl. 18, fig. 128.

Ihering's diagnosis of this species was very short: "*Le crochet est distant de l'extrémité antérieure des 27 mm. Le bord ventral est très peu convexe; la surface externe est pourvue de stries concentriques peu prononcées.*" The indications do not conform with the specimens figured, as the type, which is an incomplete inner cast lacks the external shell (as the author indicated in 1903) and the ventral portion was not preserved. The shape of the preserved half-portion, the characteristics of the anterior dorsal end, and an approximate reconstruction of the ventral margin indicate that this species does not belong to *Diplodon.* Here it is tentatively placed in *Fossula,* but since this genus and *Monocondylaea* are so closely related and fossil examples are rare, further discoveries may reveal *F. derbyi* as a very large form of *Monocondylaea* (*M. hollandi* Ortmann — a subspecies of *M. lentiformis* after Haas — has a length of 102 mm. and an altitude of 79 mm.). The outline of the species appears more rounded and less elongated than *Fossula fossiculifera,* and rather approaches *F. brasiliensis* Ihering (*F. fossiculifera brasiliensis* after Haas), but the dorsal margin is not obliquely descendent. It also has certain resemblance to *Anodontites sirionos* d'Orbigny from Bolivia (Note 30).

Actual dimensions of the fossil were not given in its original description, but the illustration of the cast, in natural size, measures 70 mm. in length, the reconstructed altitudes approximately 50 mm., and the

umbo 21 mm. behind the anterior margin, with the notch between them 7 mm. below the umbonal line (type in MACN).

Living species of *Fossula* are mainly from southern South America, at least south of the Amazon, although Pilsbry and Olsson (1944:89) described *F. venezuelensis* from the Guarico River, a species bearing some resemblance to *derbyi* but more elongated. Apparently the species of *Fossula* present many intergradations, since Bonetto (1966) assumes that *F. balzani* Ihering and *F. balzani mattogrosensis* Ihering should be integrated with *F. fossiculifera*. Olazarri (1964) indicated *fossiculifera* for several localities on the Cuareim River (northwestern Uruguay) between Artigas and the Uruguay River.

The age of *F. derbyi* was uncertain. It was taken from strata of Santa Maria do Boca do Monte, Río Grande do Sul, Brazil. The formation was first designated as a Triassic sandstone with characteristic reptiles *(Scaphonyx),* and in Ihering's estimation *F. derbyi* was Cretaceous. It is most likely an upper Tertiary species.

Subfamily ANODONTITINAE Modell, 1942
(= Glabariinae Modell, 1942)
Genus *Anodontites* Bruguiere, 1792

Type: *Anodontites crispata* Bruguiere

Patularia Swainson, 1840.
Glabaris Gray, 1847.
Styganodon Martens, 1900.
Pachyanodon Martens, 1900.
Ruganodontites Marshall, 1931.

DESCRIPTION: Valves not gaping (or very little), with edentulous hinge; periostracum marked with creases or folds of varied structure (Note 31); foot regular; supranal aperture distinct; prismatic layer wide; larva lasidium with very wide ribbon-like filament divergent at the distal end.

Although this genus is better known from the northeastern and central regions of South America, a single and rather scarce species lives in northern Patagonia, and it is abundant in La Plata River drainage area. It is unknown west of the Andes below the equator. The center of dispersion of *Anodontites* (and of the Mutelacea in general) is different from that of *Diplodon*, representing perhaps an older group which Pilsbry (1911) included in his "Eogeic" fauna, with possible but still very obscure relationships with African Mutelacea. No paleontological evidence, however, supports this view. The group from which

these naiads arose is unknown, and any relation to older, Paleozoic-Mesozoic "Naid-like" types like those described by Frenguelli (see Appendix) is very unlikely.

Although *Anodontites* is second only to *Diplodon* in abundance of South American species, reliable paleontological data is very poor. Hartt (1870) and White (1887) described some species under the generic names "*Unio*" and "*Anodonta*," from the Bahia series of northeastern Brazil, at that time regarded as Cretaceous. The species are:

?Anodontites totiumsanctorum (Hartt)

Unio (?Anodon) totium-sanctorum Hartt, 1870:351
Andonta totium – sanctorum, White, 1887:241; pl. 26, figs. 7, 8.
Type locality: Monserrat

?Anodontites hartti (White), 1887:242, pl. 26, figs. 1, 2 [as *Anodonta*]

?Anodontites mawsoni (White), 1887:243, pl. 26, figs. 5, 6 [*Anodonta*]

?Anodontites allporti (White), 1887:244, pl. 26, figs. 3, 4 [*Anodonta*]
Type locality: Pojuca

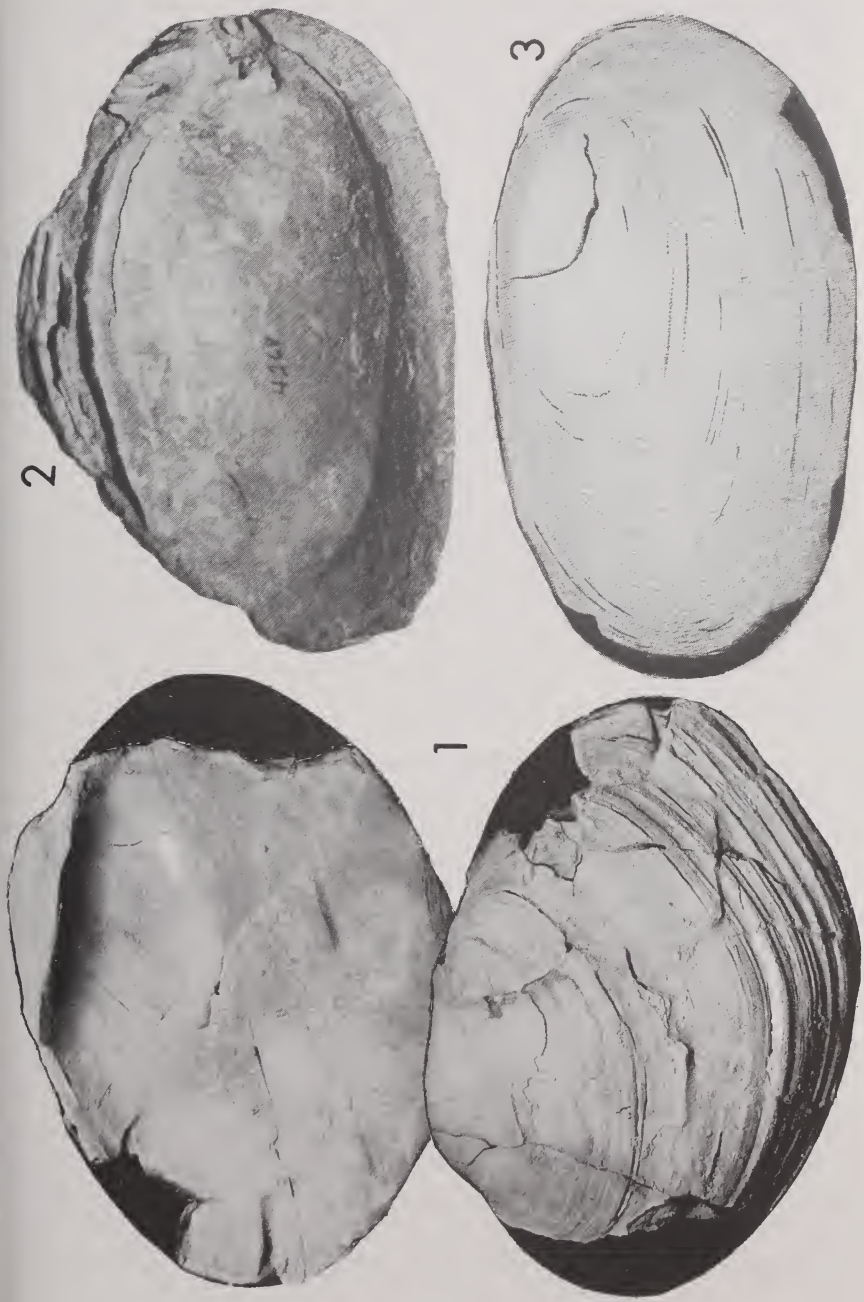
All types, according to White, are in MNRJ.

The hinges or equivalent area of these four species remain unknown. All are of very small size compared with living *Anodontites*. After their original dates no other collections were made.

Another form which also probably belongs to *Anodontites*, is *Anodonta pebasana* Conrad (1874:29, fig. 5). Its minute and acute beak and strongly inequilateral valves are different from other species known, although Conrad compared it with *A. batesi* Woodward, an equally poorly known species. The age was indicated as the Pebas formation, Pliocene, of Iquitos, Peru. It was not found by the subsequent collectors at Pebas, and it is probably the valve of a living form drifted among the eroded estuarine sedimentary debris, and allied to *A. siliquosus* Spix. De Greve (1938:19, text-figure 1) figured a fragment of an unidentifiable species, from Puesto de los Chinos at Iquitos.

PLATE 9

1. *Anodontites laciranus* (Pilsbry & Olsson). Type, x1.
2. *Diplodon diluvii* (d'Orbigny). Neotype, x1.
3. *Diplodon nordenskjoldi* (Steinmann & Wilckens). Type, x1.


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Better known, and described with more certainty within this genus, is the following:

Anodontites laciranus Pilsbry & Olsson
Plate 9, fig. 1

Pilsbry & Olsson 1935: 18, pl. 5, figs. 1, 1a.

ORIGINAL DESCRIPTION: "Shell compressed and wide, the diameter being about 43% of the length, the height about 75% of the length; moderately thick. The anterior end is rounded, posterior end produced, basal margin strongly convex in the middle. Beaks rather prominent. Sculpture of faint growth lines, and in the ventral fourth coarse wrinkles of growth and growth rests. The hinge plate is rather wide and short. Length 76 mm., height 57 mm., semidiameter 16 mm. Epidermis largely preserved."

The most conspicuous features of this species are the almost angular convexity of the basal margin, and the hinge line which, although incomplete, descends obliquely toward the anterior margin. It seems related to the *Anodontites latomarginata* group, but Pilsbry compared it with *A. patagonica*, stating that it is wider in contour. Undoubtedly the author has in mind *latomarginata,* with which *patagonica* usually has been confused (Note 32).

TYPE LOCALITY: From La Cira formation (Oligocene) at Oponcito River, near Guanabanas, Colombia. Type in ANSP.

?Anodontites olssoni Palmer

Anodontites sp., Marshall & Bowles, 1932:6.
Anodontites olssoni Palmer, 1941:406, pl. 9, fig. 7.

ORIGINAL DESCRIPTION: "Shell large, thick, umbos large, swollen; hinge line straight; posterior end slopes obliquely from the posterior termination of the hinge to the rounded posterior-ventral margin. Hinge unknown. Surface smooth with conspicuous, radiating undulating lines over the anterior portion of the shell from about the middle to almost the anterior margin, strongest ventral; irregular stages of growth. Length 65 mm., height 46 mm., thickness (both valves) 35 mm."

The inclusion of this species in *Anodontites* is made with some reservations. Marshall referred to a number of casts collected by Dr. Sheppard at the type locality of *olssoni* "with a rather thick prismatic layer," and in most "one valve has slipped toward the ventral margin so its beak is beneath the beak of the other valve." Also R. A. Liddle found many similar fragments at Azogues which Dr. Palmer compared with the type lot collected by Olsson at Biblian. From all of this Dr.

Palmer inferred that the species is rather common in that complex. As the slipping of one valve below the other seems to be a regular rather than a circumstantial feature (a condition comparable with that known in *Erodona*) and as the hinge is unknown (Palmer's observation was deduced from the exterior), the generic position cannot be totally certain. The external features, however, are like those in *Anodontites*, although they can be also related to *Leila*.

TYPE LOCALITY: From Biblian sandstone, NW. of Azogues, province of Canar, Ecuador, Lower Miocene. Type in PRI.

Subfamily LEILAINAE

Genus *Leila* Gray, 1840

Type: *Anodonta blainvilleana* Lea

Columba Lea (not Linnaeus)

Haplothaerus Conrad

Dr. A. Bonetto (personal communication), having completed studies on the anatomy and the larval cycle of *Leila*, concluded that it forms a distinct family, separated from the Mycetopodidae in the Mutelacea.

Leila capax (Conrad)

Haplothaerus capax Conrad, 1874b:83, pl. 12, figs. 1-3.

Only a fragment is known of this shell, which probably belongs to one of the living species, and the piece does not permit a correct identification. The genus, however, is undoubtedly *Leila*, by its external features and shape. It is thick, with a broad hinge area, as is sometimes seen in *L. castelnaudi* Hupe from the Upper Paraguay River.

Conrad received the fragment from James Orton, who collected it at Iquitos, Peru, indicating Pebas formation, Pliocene, but there is not assurance that it was taken "in situ" in those strata.

Subfamily MYCETOPODINAE

Genus *Mycetopoda* d'Orbigny, 1835

Type: *Anodon siliquosum* Spix

= *Mycetopus* d'Orbigny, 1847

The area of *Mycetopoda* is that of the La Plata River basin, the rivers of the Atlantic slope of southern Brazil, and the San Francisco

River. It has not been found as a fossil in South America, but Pilsbry described *M. diluculi* from the Triassic of Pennsylvania in the same strata with *Diplodon* (see discussion on page 192).

Superfamily SPHAERIACEA

Family CORBICULIDAE (Cyrenidae Lamarck, 1818)

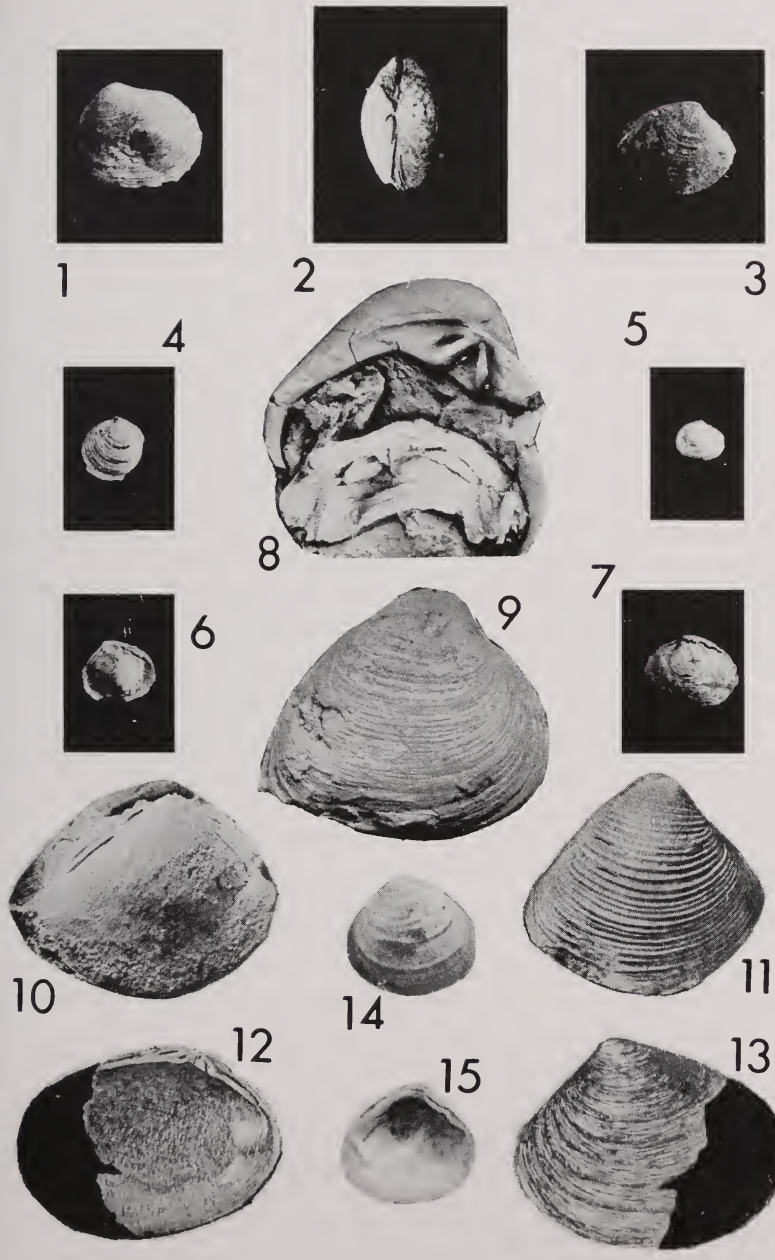
In South America the living Corbiculidae are mostly represented by two genera: *Neocorbicula*, distributed in the eastern section from the Guianas to La Plata River drainage area, and *Polymesoda*, a genus typical of the southern United States and Central America descending into Venezuela, with very rare species indicated for Chile. Among fossils, some records belong to *Neocorbicula*, and one species to the genus *Sogamosa*, which is closer to Polymesoda. Ihering (1907b) also distinguished *Corbiculella* in the Miocene. The classification of these neotropical Corbiculidae attends to the characters of the pallial line and hinges. Most of the species (living) listed by Prime in 1865 as "*Corbicula*" fall in the *Neocorbicula* group, and those mentioned by the same author under "*Cyrena*" are *Polymesoda*. In relation to the Old-World *Corbicula*, the differences are as follows:

	With pallial sinus	Without sinus	Lateral teeth crenulated	Teeth not crenulated	Without lateral teeth
Corbicula		X	X		
Polymesoda	X			X	
Neocorbicula	X		X		
Corbiculella		?		X	
Sogamosa	?				X

Some fossil South American species were referred to *Eriphyla*, a genus of uncertain position (see page 100).

PLATE 10

1-7. *Neocorbicula pehuenchensis* Doello-Jurado. Type, x1.
8,9. *Sogamosa cyrenoides* (Pilsbry & Olsson). Type, x1½.
10. *Neocorbicula pacchiana* (Palmer). Type, x2.
11. *Neocorbicula cojintamboensis* (Palmer). Type, x2.
12,13. *Corbiculella tenuis* Ihering. Type, x2.
14,15. *Neocorbicula salobris* (Ihering). Type, x1.


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Genus *Neocorbicula* Fischer, 1887

Type: *Tellina limosa* Maton
= *Cyclas variegata* d'Orbigny

= *Cyanocyclas* (in part) authors.

This differs from *Corbicula* by having a pallial sinus and longer siphons, but it has the same crenulations on the lateral teeth. Living species are viviparous (see Parodiz & Hennings 1965). The genus is exclusively neotropical, while the Old-World *Corbicula* forms a belt from West Africa to Melanesia, extending 45° north and 45° south of the equator, and including Europe, Central Australia, and Tasmania, but not New Zealand.

Neocorbicula pehuenchensis (Doello-Jurado)
Plate 10, figs. 1-7

Corbicula pehuenchensis Doello-Jurado, 1927:409, pl. 8 (in Wichmann 1927), figs. 53, 54; pl. 9, fig. 58. Frenguelli 1930a:29, 31. Feruglio 1949, 1:240, 283, 286.

Corbicula dinosauriorum Doello-Jurado, 1927:409, pl. 8, fig. 52, pl. 9, figs. 59, 60. Frenguelli 1930a:29, 31. Feruglio 1949, 1:240, 283, 286.

Similar to the living species from the Uruguay River, it has an equilateral, sub-or-trigonal form, concentrically striated but with umbo less prominent. The concentric-costular marks (variable in number from 10 to 20) are sometimes well spaced or may be compact, in which case they are numerous. The shell may be quite elongated, like most *N. limosa,* or almost subquadrate as in *limosa* "form delicata." In living *Neocorbicula* many named "species," by their form or sculpture, proved to correspond, in a series of variable populations, to forms of a same species, *limosa*. Their great variability is a result of their way of reproduction (see Parodiz & Hennings 1965), and the different fossil specimens, of *pehuenchensis* observed offer the same range of variations, including *dinosauriorum*. The type and name here selected is that of fig. 57 of Wichmann, Doello-Jurado, which shows the unmistakable, characteristic crenulations of the lateral teeth.

The type measures 12 mm. x 10 mm. and its half-diameter (one valve) is 3 mm. Other paratypes are larger, reaching 18 mm. x 15 mm. x 10 mm. Comparatively it attains an average size half that of *limosa*. The types and paratypes were collected by Dr. R. Wichmann in 1916, and figured for the first time in 1927, under the numbers mentioned in the same

volume of the "Boletin" of Córdoba Academy by Doello-Jurado when describing the species. Other external casts in matrix from the same strata and locality were previously collected by Wichmann in 1912.

TYPE LOCALITY: Southern Cliff of the Río Negro, at General Roca (formerly Fresno Menuco) in the lower strata of the Jahuel formation (Paleocene), N.W. of the province of Río Negro (Patagonia) Argentina. Type in CM.

Neocorbicula pacchiana (Palmer)
Plate 10, fig. 10

Corbicula (Cyanocyclas) pacchiana Palmer, 1941:407, pl. 9, fig. 5.

ORIGINAL DESCRIPTION: "Shell of medium size, beaks high, shape trigonal, hinge with narrow laterals, surface entirely covered with coarse, concentric ribs. Length 26 mm., height 23 mm., semidiameter 4 mm."

TYPE LOCALITY: Near Paccha, along the Quebrada of Paccha, province of Azuay, Ecuador, in Azogues Sandstone, Upper Miocene, collected by A. A. Olsson 1936. Type in PRI.

Dr. Palmer indicated that this species came from the same formation as *Neocorbicula cojitamboensis* (which is more concave beneath the beaks). It bears resemblance to *N. cuneata* (Jonas), living in the Orinoco.

Neocorbicula dormitator (Pilsbry)

Corbicula dormitator Pilsbry, 1939:71, pl. 9, fig. 2.

Pilsbry placed this very poorly known species in *Corbicula (sensu lato)* by observing the hinge. As the teeth of both *Corbicula* and *Neocorbicula* are similar, the second replacing the first in South America, there is no doubt about its generic position. Pilsbry's short description is as follows:

"The type is the internal cast of the right valve, and in the hinge region the anterior lateral tooth of the opposite valve, and the cardinals, are visible by removal of the shell. The height and length are about equal (L. 9 mm., H. 8.3 mm., semidiameter 2.8 mm.). The anterior end is more narrowly rounded than the posterior. The fragments of pseudomorph of the shell do not show any sculpture, but they are somewhat worn."

TYPE LOCALITY: Limestone of Miraflores (Mirafloran), Paleocene, at El Molino, N.W. of Potosi, Bolivia. Type in ANSP.

Neocorbicula chilensis Soot-Ryen

Soot-Ryen, 1952: 309, pl. 1, figs. 5-7 (as *Corbicula-Cyanocyclas*).

ORIGINAL DESCRIPTION: "Shell small, oval, longer than high, of faint greyish-blue tone. Umbo slightly prosogyrate, anterior dorsal margin nearly straight, sloping; posterior dorsal margin slightly convex; posterior and ventral margin rounded. Sculpture consisting of fine concentric stripes, especially distinct on the posterior part of the valve. Hinge well developed and preserved, teeth 2a and 2b form together an inverted V, 2a is narrow and does not reach the margin of the hinge plate, 2a is strong, perhaps with a median furrow, 4b is short and separated from the nymph by a shallow furrow. The lateral P.II is long, with ridges (about 12) on the dorsal side and separated from 4b by a flattened area; A II is so worn that the dorsal ridges are invisible. The anterior impressions are indistinct and no trace of the pallial line and sinus can be seen."

Although the pallial line and sinus has not been observed, the hinge is of the same type as in *Neocorbicula limosa.* The dimensions given in the description, length 3.4 mm., height 2.7 mm., must be a printing error. Evidently they are 34 mm. x 27 mm.

The author's reference of *Cyanocyclas* from the Cretaceous of western America according to Dall, does not belong to this group (*Neocorbicula*).

The type locality was described as "from a shellbank in the bay near Punta Arenas," on the Magellan Strait, Chile. The age was indicated in general terms as Tertiary, but by the finding of other fossils (marine *Trinacria*) Soot-Ryen supports an Eocene age for some of the fossiliferous layers in the Magellanic area. But it is more probable that it belongs to the same strata as *Diplodon,* from the vicinities (Río Cóndor) which, according to Feruglio, are equivalent to the Navidadean in Chile and the "Terciario Carbonifero" in Neuquén, that is, Oligocene. It is the southernmost locality known for Corbiculidae, fossil or living. The fossil was found in a situation similar to that of many other fresh-water shells from the Tertiary (see page 28), intermingling with marine and brackish-water. The type is in NR.

Neocorbicula cojitamboensis (Palmer)
Plate 10, fig. 11

Corbicula (Cyanocyclas) cojitamboensis Palmer, 1941:408, pl. 9, fig. 6.

ORIGINAL DESCRIPTION: "Shell small, beaks high, shape trigonal; hinge with narrow laterals, surface entirely covered with coarse concentric ribs. L. 16 mm.; H. 14 mm.; semidiameter 4 mm."

Although the descriptions of this species and *N. pacchiana* indicate very similar characteristics, *N. cojitamboensis* is proportionately higher, with more prominent beaks, very conspicuous concentric sculpture, and smaller size. Palmer compared these two species with *N. undulata* Marshall, which has a similar sculpture, but that species from the Uruguay River proved to be one of the forms of the very variable *N. limosa* (Maton) (see Parodiz-Hennings 1965).

TYPE LOCALITY: From bituminous limestone of Arroyo Potrero, West of Cojitambo, in the vicinity of Cuenca, Ecuador (the same beds contain *Hemisinus peyeri*). The strata are middle Miocene. Collected by R. E. Dickerson, 1927. Type in PI.

Further studies, based on more abundant materials, may show that the differences between *N. pacchiana* and *N. cojitamboensis* were as variable as those known in living species, i.e., *N. limosa*, and co-specific. At present, following Palmer, they are distinguished as separated species.

Neocorbicula stelzneri, new species
Plate 11, figs. 2, 3

"*Corbicula stelzneri*" of authors *(nomen nudum)*

Under the name "*Corbicula stelzneri*" Doering, many geological works referred to some fossil bivalves found by A. Stelzner in 1872 at San José, in the Valley of Santa María, Catamarca ("Kreideformation von Tucumán and Catamarca" Stelzner 1885). This "species" was neither described nor figured, being a *nomen nudum*, and the only assumption Doering could make was that it must be a "representative of a subgenus found in Río de la Plata."

Casts of these bivalves were obtained by Frenguelli in 1927, and sent for determination to the malacologist, Prof. Doello-Jurado (then director of the Argentine Museum of Natural Sciences), who informed the collector that they actually belonged to the same group of "*Corbicula*" as those found in La Plata river system. When I revised the collections of that museum I did not find such specimens, and Frenguelli was unable to provide more. But he agreed (personal communication) that the species in question was in fact a *nomen nudum*, and it was as such that he mentioned the fossils (1937: 420) which he recognized from Arroyo Calavera and Bajo Amenida, in the Catamarca section of the Valley of Santa Maria (Note 21). During a recent visit to northern Argentina (1966) I obtained a lot consisting of numerous

specimens, which offers the opportunity to formally describe *stelzneri* as a new species of *Neocorbicula*. Since a *nomen nudum* has no status, and does not preoccupy (and in addition, as it was given originally as "Corbicula," not *Neocorbicula*), that name is preserved, to avoid possible confusion in the geological literature.

DESCRIPTION: Shell oblong-rounded, slightly inequilateral in the type but in other specimens the prosogyrate position of the umbo is more accentuated. Moderately thick (valves at middle section 0.75 mm. thick). Ventral margin normally curved but sometimes angulated and when such angle exists it is closer to the anterior portion; anterior margin a little extended and curved; posterior margin descending rapidly from the ligamental area, forming an obtuse angle behind, and then curving into the ventral margin. Transversal diameter between valves almost half the total length. Surface profusely covered with wrinkles of growth, which sometimes look like imbrications and are very strong at the lower section of the valves. Most of the specimens are laterally compressed, possibly by pressure of the sediment, but a few better-preserved fragments have a rather wide escutcheon area. The short tresilium is visible and the lunule is small, but deep and conspicuous.

DIMENSIONS (IN MM.)

	Length	Height	Lesser diameter	Distance, umbo to: posterior slope	anterior slope	Diameter between valves
Type	25.5	22.2	10.5	15	13	—
Paratype						
A.	24.5	20.5	—	—	—	10.5
B.	24.5	20	—	—	—	10.5
C.	24.4	20	—	—	—	12.7
D.	23.5	21	—	—	—	(single)
E.	21.5	19.5	—	—	—	11
F.	18.4	18.5	—	—	—	8.2
Average dimensions	22.9	20.2	—	—	—	11.7

Neocorbicula stelzneri is close to *N. limosa* (the type of the genus), but compared with the latter is more elongated, and its umbos are less swollen, but more pointed and slightly nearer the anterior edge. There is a posterior ridge, more marked in some specimens. The concentric lines of growth are stronger, the escutcheon less raised, and the dorsal margin flatter with a larger ligament. It differs from *N. paranensis* by being considerably less inflated, thinner, and having a finer hinge.

TYPE LOCALITY: East of Santa María, in the Santa María Valley W. of Sierra Aconquija (near the limit with Tucumán), province of Catamarca, Argentina;

from "Estratos Calchaqueños," Calchaquian (or Santamarian Frenguelli), middle Miocene. Collected by R. Herbst. Type and 150 paratypes at IML; 30 paratypes, including those measured, at CM (See Note 21).

Most of the specimens have both valves cemented by a very hard, gray-greenish sandstone matrix. No pallial sinus was observable, but their identification within the genus *Neocorbicula* confirms Doering's references to similarity to the Platean species. In one specimen the texture of the matrix shows an alveolar structure as if smaller valves had been originally embedded. These correspond to embryos, like those always present in specimens of the living species of this genus, which is characterized by self-fertilization. The original matrix is sometimes replaced by crystallized infiltrations in the interior of the fossil which, if sectioned, shows the aspect of a geode. To this same species very probably belongs the "Cyrena" referred to the "Serie margoso-yesifera" by Bonarelli & Pastore, 1916.

? *Neocorbicula salobris* (Ihering)
Plate 10, figs. 14, 15

Cyrena salobris Ihering, 1907b: 413, pl. 16, fig. 109; 1914: 41. Feruglio 1950, 3: 131.

Shell small, suborbicular, convex, rounded at front and subtruncate posteriorly, Ventral margin convex. Surface smooth. Posterior lateral tooth on the left valve, short and elevated; anterior also elevated and well separated from the cardinal; both laterals are without crenulations. The cardinals are divergent, the median stronger. Pallial sinus small. Length 17 mm., height 15.5 mm., diameter 5.5 mm.

Ihering thought that this "Cyrena" should be included in subgenus *Pseudocyrena* on account of its non-crenulated teeth. But the true position of the species remains uncertain, since the scarcity of the material precludes any conclusion. It may be that the lack of crenulations shown in the type is due to the worn condition of the fossil. It is listed here under ?*Neocorbicula* because of the general similarities. The shape of the shell recalls *Corbicula astartina* from western Africa, but *Corbicula, sensu stricto*, has no pallial sinus.

TYPE LOCALITY: Sierra Laziar, 50 km. N.W. of Puerto Deseado, Sta. Cruz, Patagonia; from a terrace, 170-180 meters above sea level, of the middle Pliocene (Lazarian). Type in MACN.

The fossil mollusks of "Laziarense," were studied mainly by Feruglio (1933, 1950). It is worth notice that, among the 33 marine species of shells indicated for this level, only *salobris* is fresh-water and brackish-

water. It may be suspected that its appearance there was accidental, by drift. No other Corbiculidae are known from fresh-water beds of the Pliocene of Patagonia.

Neocorbicula (undetermined species)

Pilsbry (1944: 146) made references to "remains of *Corbicula (Cyanocyclas)* from the Red Beds [of the Pachitea River, Peru] mainly in the form of internal casts, insufficient for specific comparison with those of the Cuenca Basin or elsewhere." These materials are:

From San Antonio Pachitea River; numerous internal casts without traces of shell, and no hinge impressions. Many of them are much compressed and distorted (1944: pl. 9, figs. 9-12).

From two miles downstream at Santa Isabel Island, Pachitea River (1944: pl. 11, fig. 37).

The age of the "Red Beds" of the Pachitea River in Peru have been, tentatively, considered coeval with La Cira formation of Colombia, upper Oligocene – lower Miocene. "Such differences as appear between La Cira, Pachitea and Cuenca beds, are more likely owing to their geographic separation than to any material difference in age. The Pachitean fauna is very incompletely known" (Pilsbry).

I also have found an undetermined cast of a small *Neocorbicula* (Plate 11, fig. 6) in the matrix containing *Paleoanculosa araucana* (Philippi), of the "Terciario Carbonifero" below Concepción formation, Chile, which are upper Paleocene. It apparently represents a distinct species, of medium size, but the condition of the fossil permits no description.

Marly sandstone from the "Calcareo-dolomitico" of Purnamarca, 20 kilometers south of Tilcara, province of Jujuy, Argentina, contains *Neocorbicula* and *Potamides.* The conglomerate is identical with that illustrated by Frenguelli (1936:309), fig. 85) from Alemania in southeastern Salta (Plate 11, fig. 1).

PLATE 11

1. Marly sandstone from the Paleocene of Purnamarca, Jujuy, Argentina, with casts of *Neocorbicula* and *Potamides potosensis* (d'Orbigny). x1.

2,3. *Neocorbicula stelzneri* Parodiz. 2. Type, 3. Paratype, x1¾.

4. Sandstone conglomerate from Rio Percy, Esquel, Chubut, Argentina, with *Diplodon chilensis.* Oligocene. x1½

5. *Lymnaea klappenbachi* Parodiz. Type, x2.

6. *Neocorbicula* sp. from strata of Lonquimay at Concepcion, Chile. x2½.


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Subgenus ?*Corbiculella* Ihering, 1907

Type: *Corbicula tenuis* Ihering

Ihering, 1907b: 462, 469.

The description of *Corbiculella* was implied, in that of *Corbicula tenuis,* as a subgenus. It differs from *Neocorbicula* by its non-crenulated lateral teeth (a character also found in *Polymesoda* and *Sogamosa* but differing from these genera in other features: Ihering commented, "I see no indication of a pallial sinus." Actually he could not have been certain whether or not the species has a pallial sinus, because it is not observable in the fossil fragment of the half-valve used as type. The fossil was found in an area in which living species of *Neocorbicula* today are abundantly represented by variable populations (Paraná River), but the fossil apparently differs substantially from these and perhaps corresponds to an extinct group.

Neocorbicula (Corbiculella) tenuis Ihering

Plate 10, figs. 12, 13

Ihering, 1907b: 468, pl. 18, figs. 130a, 130b. 1914:41.
Frenguelli, 1920: 108, 120. 1937:486.

DESCRIPTION: Shell oblong, thin and fragile, with inconspicuous umbo, ventral margin convex, dorsal margin descending obliquely; anterior margin obtusely triangular. Surface smooth with weak concentric lines of growth. Hinge cardinal with a double — or bifid — cardinal on the right valve, lateral teeth short and without crenulations. The size was estimated by Ihering from the incomplete valve as: length 51 mm., height 12 mm., and semidiameter, 3.3 mm.

The type figured by Ihering is half of two left valves in external and internal views. Figure 130a, which agrees better with the description and may be considered the type, is more like *Neocorbicula.* Figure 130b differs in its more oval shape, and in having margins perfectly rounded. Ihering declared that the two figures represent different views of the same specimen, but this does not seem possible, since the outlines and size are entirely different (only the broken line seems to match).

The materials were collected by Ihering himself, from strata in the ravines of the right side of the Paraná River, where *Diplodon fraus* was found. In revising Ihering's collection (now at the Argentine Museum, Buenos Aires) I did not find any specimen with that reference. In 1914 Ihering listed in his "Catalogue" (page 41), "4 cotypes from Bravard collection," in addition to casts of valves in matrix obtained by the geologist Santiago Roth at La Paz, Entre Ríos.

Frenguelli (1920, 1937) said he found "thousands of badly preserved specimens" in fluvial deposits of Paraná at the Quarry of Izaguirre (No. 5 of Frenguelli's stratigraphic scale). He thought the species should be referred to *Pseudocyrena*.

The age of *N. tenuis* is lower Pliocene. As in the case of *N. stelzneri*, which was mentioned by many geologists as abundant *in situ*, this form is also very rare in collections. It deserves a complete revision based on new and better materials.

Genus *Sogamosa* Pilsbry, 1935

Type: *Sogamosa cyrenoides* Pilsbry

DESCRIPTION: "Shell similar to *Polymesoda* externally; hinge broad, with three divergent cardinal teeth in each valve; no lateral teeth on the flat hinge plate. We are uncertain as to the systematic position of this peculiar clam, but temporarily refer it to the family Corbiculidae. The dentition has some resemblance also to that of some Donacidae, such as *Iphigenia*. Whether a pallial sinus is present could not be observed" (Pilsbry & Olsson, 1935: 18).

Sogamosa cyrenoides Pilsbry & Olsson, 1935:18, pl. 4, figs. 4-7
Plate 10, figs. 8, 9

ORIGINAL DESCRIPTION: "Shell plump, subtriangular, about as high as long, moderately solid. The hinge line is strong, arched. The prominents beaks are in front of the middle, contiguous and turned forward. No lunule or escutcheon present. Posterior ridge obtusely subangular. Sculpture of fine, rather short, concentric striae. Hinge plate broad, each valve with three divergent cardinal teeth, and no laterals. In the left valve, the anterior cardinal is highest, wedge-shaped, the posterior lowest and near the middle tooth. In the right valve, the middle tooth is large, stout and separated by a wide socket from the low, curved, posterior tooth. The anterior right cardinal is long and narrow. The flat hinge plate behind the cardinal is rather long tapering posteriorly, with no trace of a lateral tooth. In front of the cardinals [the hinge] is short and toothless. Muscle and pallial impressions not seen. The ligament is short and external, its limit marked by an impressed line. L. 21.5 — 26 mm., H. 23-23.5 mm., semidiameter 9 mm." (Pilsbry).

TYPE LOCALITY: 80 meters N., 40 meters W. from the mouth of the Quebrada Cabezoneras branch of the Sogamoso River (W. of the Magdalena), Colombia, in upper Eocene strata of Los Corros (Corrosian). Type in ANSP.

Externally, *Sogamosa cyrenoides* is like *Polymesoda arctata* (Deshayes), a living form of Venezuela, but differs in the total absence of lateral teeth and in the relative sizes of the cardinals. It was found in very hard sediments, also containing *Diplocyma* and *Hemisinus*, suggesting estuarine or brackish-water conditions. The genus is apparently extinct.

Although still of uncertain taxonomic position, the genus *Eriphyla,* with two Paleocene species, probably related to the Corbiculidae is discussed below.

Genus *Eriphyla* Gabb, 1864
Type: *E. umbonata* Gabb
(Chico formation, California)

Eriphylopsis Meek, 1876

?*Dozya* Bosquet, 1868.

The shells of *Eriphyla* are of small size, are like *Astarte,* and are similar to *Crassinella* but with external ligament and resilum. Dall used it as a subgenus of *Crassatella,* or ancestral to *Crassinella. Eriphyla* also recalls *Remondia,* in which the ligament is partly external. The two species from the South American Paleocene, *Eriphyla sehuena* and *E. miraflorensis,* resemble the type of *Crassinella, C. martinicensis* d'Orbigny. Some of the characters of the type of *Eriphyla* are not observable in these fossils, thus the generic indication can be only provisory, and is given here because the generic name *Eriphyla* is profusely mentioned in paleontological works on Patagonia. While *Crassinella-Crassatella* are marine, *Eriphyla* are purely brackish-water and always associated with *Potamides.* Pilsbry also used *Eriphyla* as a subgenus of *Crassatella* when he described the living *C. maldonadoensis* from Uruguay. On the other hand, *Crassinella dalli* Ihering from the Oligocene marine of Patagonia appear as a very different shell from *Eriphyla.* Although sometimes placed among the Crassatellidae, the family position of *Eriphyla* is still dubious, and relationship with Corbiculidae where the concentric ribs became obsolete in truly fresh waters is not improbable (Note 41). Certain Asiatic species of *Corbicula,* as *C. sumatrana* Clessin, have shape and sulcation similar to *Eriphyla.*

The species *Eriphyla sehuena* (Ihering), in MACN, and *E. miraflorensis,* new name, are quite similar, showing that this group was widely distributed in the Paleocene from Patagonia to Peru, as were other coeval genera *(Potamides, Pyrgulifera).* This group apparently is very old in the southern region. Feruglio (1950) mentioned several species of *Eriphyla* from the Mesozoic of Patagonia and Tierra del Fuego:

Eriphyla aff. *agrioensis.* Upper Jurassic of Cerro Castillo, southeastern Santa Cruz.

Eriphyla argentina Burckhardt. Las Lajas, at the bend of Río Agrio, Neuquén (Note 49).

Eriphyla drygalskyana. Cretaceous of Leticia, Atlantic coast of Tierra del Fuego.

Eriphyla sp. Middle Cretaceous of Lake San Martín.

Eriphyla sehuena (Ihering)

Astarte sp. Ihering, 1897:316.
Venus or *Astarte* sp. Ihering, 1899:64. Ameghino, 1906:54.
Corbula sp. Ihering, 1903:209.
Corbula sehuena Ihering, 1907b:51, f. 5. Frenguelli, 1930a:39.
Eriphyla sehuena, Feruglio, 1950, 1:258, 272, 274.

DESCRIPTION: Shell subtriangular, very little inflated and slightly inequivalve. Umbo subcentral, closer to the anterior margin. Basal margin rounded. Surface ornamented with concentric costulae, slightly elevated, varying in number from 15 to 20, separated by wide intervals. Length 15 mm., height, 13 mm., diameter, 7 mm.

Ihering consulted with Dall and Pilsbry about the generic position of this species, and was advised to place it in *Corbula.*

TYPE LOCALITY (restricted): Mata Amarilla, on the Sehuen — or Chalia River — of Southern Santa Cruz, Patagonia. Sehuenian (facies of the Jahuelian), Paleocene. Type in MACN.

Eriphyla **miraflorensis,** new name

Cyrena cf. *exarata* Dunker, in Fritzsche, 1924:25, pl. 1, fig. 5.
Ahlfeld ,1946: pl. 7, fig. 6.

This species is very close to *E. sehuena,* of the same age, but smaller and proportionally shorter (9mm. x 5 mm.), with fewer concentric ribs (10 to 15). It has the same triangular form with rounded lower margin, but the ribs grow wider at the base. Fritzsche did not mention Ihering's species for comparison, preferring a specific name corresponding to a European form described by Dunker in 1846. But Fritzsche referred its similarities to *Astarte* and *Corbula,* as Ihering did with *E. sehuena.* Being coeval, although widely allopatric, *E. miraflorensis* and *E. sehuena* may be subspecifically linked. However, this form, which is not *exarata,* should receive a new name, and *E. miraflorensis* is adopted from the well known fossil locality studied by Steinmann, Pilsbry, and Ahlfeld.

TYPE LOCALITY: Limestone of Miraflores, near Potosí, Bolivia, in the Upper Puca formation (Mirafloran) Paleocene. Type in NR.

From the Paleocene complex of northern Argentina and Bolivia, Fritzsche mentioned other species of *"Cyrena"* (indicated as Cretaceous), all under specific names given by Roem and Dunker for European species. These species were briefly mentioned, without illustrations, and do not permit further identification. Probably they will be rediscovered, and if so they should be given new names. They were indicated for the following localities:

Yavi, 90 km. N. of India Muerta, Prov. Jujuy, Argentina. (affinis *Cyrena zimmermanni* Dunker after Fritzsche). Found together with "Lymnaea" and "Paludina."

Lechugillas, near Sucre, Bolivia (aff. *Cyrena venulina* Dunker). With *Potamides.*

Comon, SW. of Potosí, Bolivia (aff. *Cyrena zimmermanni* and *C. dorsata* Dunker, *C. nuculaeiformis* Roem).

Miraflores (aff. *C. zimmermanni* Dunker). It was with *Eriphyla miraflorensis* and probably is the same species.

If all these "species" in Fritzsche's judgment belonged to the same genus *("Cyrena")*, then it is evident that the habitat of the *Eriphyla* is mainly fresh water and sometimes brackish-water.

Family SPHAERIIDAE

Genus *Sphaerium* Scopoli, 1777

Type: *Tellina cornea* Linnaeus, 1758.

Sphaerium ativum White

White, 1887: 240, pl. 26, fig. 9.

DESCRIPTION: Shell small, subovate in marginal outline, moderately inflated; valves have nearly uniform convexity; beaks slightly elevated, situated about one-third of the full length of the shell from the front. Surface marked by numerous, regular, concentric raised lines; the hinge is not known but the shell seems to be that of a true *Sphaerium.* Length 6 mm., height 4 mm. The specimens are more or less distorted by pressure, but the natural shape is essentially as described above. The species is notably like *S. bahiensis* Spix, which is now living in the fresh waters in the vicinity of Bahia. (White: 240, 241.)

TYPE LOCALITY: Vicinity of Pojuca Station, 85 km. N. of Bahia, Brazil. The stratum was indicated by White as Cretaceous, but probably it is lower Paleocene (see page 15), and belongs to the same series in which Allport, Hartt, and White found *"Anodonta."* No further references have been made of this species since its description. Type in MNRJ.

Genus *Pisidium* Pfeiffer, 1821

Type: *Tellina amnica* Müller, 1774

Pilsbry (1939:71) refers two specimens of this genus, resembling *P. titicasensis* Pilsbry (the condition of the materials did not permit

description). These were found near El Molino, Potosí, Bolivia, in the strata of Miraflores with *Dorysa andicola* and *Neocorbicula dormitator*.

GASTROPODA

Order MESOGASTROPODA
Superfamily CYCLOPHORACEA
Family APEROSTOMATIDAE
(Aperostomatinae Baker = Poteriinae)
Genus *Poteria* Gray, 1850
Type: *Turbo jamaicensis* [Chemnitz] Wood, 1826

= *Platystoma* Morch, 1850 not Meigen, 1803.

Subgenus *Pseudoaperastoma* Baker, 1943
Type: *Cyclostoma inca* (d'Orbigny)

= *Neocyclotus* (in part) Crosse & Fischer, 1886

DESCRIPTION: "Shell depressed, conoid, or with last whorl descending markedly (cf. *Poteria confusa*); usually with darker spiral bands; growth lines comparatively delicate and regular. Central America to Brazil [and Bolivia]" (Baker, 1923).

Fischer & Crosse included *C. inca* d'Orbigny in their genus *Neocyclotus*, which according to Baker, now stands for the species Bartsch placed in *Aperostoma, sensu lato*. The definition of *Pseudoaperastoma* as the "group of *Cyclostoma inca*," without name, was given by Baker in 1923, the name was given in 1943. D'Orbigny found *C. inca* on the eastern slope of the Andes, from Colombia to Bolivia, and east to Brazil, in dense forests. Although empty shells are commonly found, it has been difficult to collect them alive. During the dry season the mollusk buries itself deep in the ground and becomes active only during the periods of heavy rain.

Poteria, sensu stricto, is known from the Miocene of Jamaica. *Pseudoaperostoma* was probably a very early Neogene migrant.

Poteria (Pseudoaperastoma) bibliana (Marshall & Bowles)
Plate 16. figs. 2, 3

Pomacea bibliana Marshall & Bowles, 1932:4, pl. 1, figs. 4-5.

This species does not belong to *Pomacea (= Ampullarius)* or any genus of Ampullariidae. The shell is very similar to *Poteria inca* d'Orbigny. It has 3 to 4 whorls sharply increasing in size, the spire is very flat, and most of the shell is composed of the body whorl, almost cari-

nated at the periphery, with a widely expanded aperture. Above the angulated periphery the whorl is decidedly convex, and below, it descends obliquely toward the base of the aperture. The shell is one-third wider than it is high: diameter 30 mm., height 20 mm.

TYPE LOCALITY: Biblian, province of Canar, Ecuador, in lower Miocene strata (Biblian), coeval with those of the Real series of Colombia. Type in USNM.

It was found with *Diplodon guaranianus biblianus, Doryssa bibliana* and *Potamolithoides*. A truly terrestrial snail, it probably was carried into fresh-water deposits by heavy rains.

Superfamily VIVIPARACEA
Family VIVIPARIDAE Gray, 1847 (Paludinidae)
Genus *Lioplacodes* Meek & Hayden, 1864

Type: *L. veternus* Meek & Hayden
Jurassic, Wyoming.

The name *Lioplacodes* was introduced by Meek & Hayden for Jurassic "*Viviparus.*" Branner (1904) remarked that it is very difficult to separate it from *Lioplax* (see revision of *Lioplax* by Clench & Turner 1955), and said it differed from the latter by its more elongated form and smaller body whorl. *Lioplax* itself differs from other Viviparidae by its operculum with concentric nucleus instead of paucispiral, a character unobservable in fossils. The species here discussed are rather like *Viviparus,* and were described under that name, or under *Paludina.* The name *Lioplacodes* as used here is tentative only, and with the reservations manifested by Clench regarding fossils of these groups. Other species of *Lioplacodes* were referred by Teng-Chien Yen (1946) for the Cretaceous of Wyoming: *L. cretaceous* (Stanton) and *L. convexiculus* Yen.

Doello - Jurado (1922) was the first to suggest the relationship of North and South American Viviparidae as resulting from a probable southward migration during the Cretaceous-Tertiary transition. Fossil species are known from Brazil, Bolivia, Chile, and southern Argentina (Patagonia). *Lioplacodes* became extinct in South America early in the Tertiary. The genus *Viviparus, sensu lato,* formerly included many forms with almost world-wide distribution, but in recent studies it has been divided into several continental taxonomic groups. These are not part of the late Mesozoic fauna of the Old World, and have been known only since the Pliocene from southeastern Europe. Fossil records from Australasia are only Pleistocene (*Notopala* and *Centropala* Cotton).

Lioplacodes feruglioi, new species
Plate 12, figs. 1, 3

Viviparus wichmanni (in part) Doello-Jurado, 1927: figs. 72-75.

DESCRIPTION: Shell imperforate or scarcely rimate; elongate with high spire. The entire shell should have had 5 or 6 whorls, but the apex is fractured in most of the specimens. Those better preserved have 4 or 5 whorls, the last one less globose than in *Lioplacodes wichmanni* and the penultimate one higher. A moderate peripheral angulosity is observable in a few, smaller specimens, apparently juveniles. The suture is well marked and sometimes has a margination produced over it at the base of the whorl. Surface has very conspicuous waving folds of growth. Aperture nearly circular.

The type, with 5 complete whorls, measures 29 mm. x 19.5 mm. Because of the broken nuclei in all other specimens of the lot, altitude was taken by comparison of the last two whorls (altitude in the type is 25 mm.).

TYPE LOCALITY: Lowlands of Lenza Niyeu, central Río Negro province (northern Patagonia), in strata of the Jahuelian, Paleocene; collected by R. Wichmann 1923; 27 paratypes; observed range: length 25/32 mm., diameter 14.5/18 mm., ratio length/diameter 1.30. Type in CM; paratypes in MACN.

The sample lot on which this species is based was referred by Doello-Jurado (1927) to his *Viviparus wichmanni,* with the implication that the original type lot (described five years earlier) were underdeveloped forms of the same species. Comparison of *L. feruglioi* with the larger juveniles of *L. wichmanni* reveals that the differences are obvious. *L. wichmanni* (the type of which is a fully grown specimen) scarcely reaches the proportions of young *L. feruglioi.* The distribution of length and width when plotted in a chart shows insignificant overlapping between the frequencies. Apart from differences in proportions, there are other conspicuous characteristics for the specific separation, as the suture, the waving lines, the more-elongated spire, and the less-inflated body whorl. *L. feruglioi,* shows a tendency to longer individuals without modifying the average width. These differences were noticed by Wichmann (who collected the samples at separated localities and dates), and according to his comments: "these strata contained different species of *Viviparus,* one of them from the río Negro ravines at Gral Roca described by Doello Jurado as *wichmanni*" (1927:403).

This species is named in memory of my late friend Dr. Egidio Feruglio, author of many important contributions on the geology of Patagonia.

Lioplacodes wichmanni Doello-Jurado, 1922
Plate 12, figs. 4,6

Viviparus wichmanni Doello-Jurado, 1922: 329, figs. 1-3; 1927: 412 (the references to figs. 72, 73 correspond to *L. feruglioi*). Frenguelli, 1930a: 29, 31. Feruglio, 1950, 1: 240 283, 286.

ORIGINAL DESCRIPTION (translation): "Shell turbinoid, imperforated, spire elevated; whorls more convex in young specimens than in adults, 4 in number in the figured specimen (apex broken); another specimen of only 13 mm. wide, with 4½ whorls. The last whorl (in the type) is slightly flattened and depressed at the base, with a semi-angulose outline. Suture impressed. Aperture regularly circular. Surface smooth with very weak [straight] lines of growth."

TYPE LOCALITY: South cliff of Río Negro at General Roca (formerly Fresno Menuco), province of Río Negro (northern Patagonia), Argentina, in strata of the Jahuel formation, Paleocene. Type in CM.

DIMENSIONS: Type: length 19.5 mm., diameter 21-15 mm., spire 10 mm. Paratypes: 15.5 mm. x 12.8 mm.; 14,8 mm. x 12 mm.; 12.2 mm. x 11 mm. Mean of ratio length/diameter: 1.16. The dimensions given by the author for the type belong to a larger specimen which, although not figured, was very similar to that in fig. 1. There is also some mistake in the diameter given (26 mm.). This cannot be more than 16 mm.

L. wichmanni differs from *L. feruglioi* in its more globose and shorter outline, smaller general proportions, lack of the waved lines of growth, obtuse spire, and in being more like *Viviparus* than the other *Lioplacodes*.

?*Lioplacodes lacerdae* (Hartt), 1870

Paludina sp., Morris, 1859, Quar. Jour. Geol. Soc. London: 16, pl. 14. fig. 2.

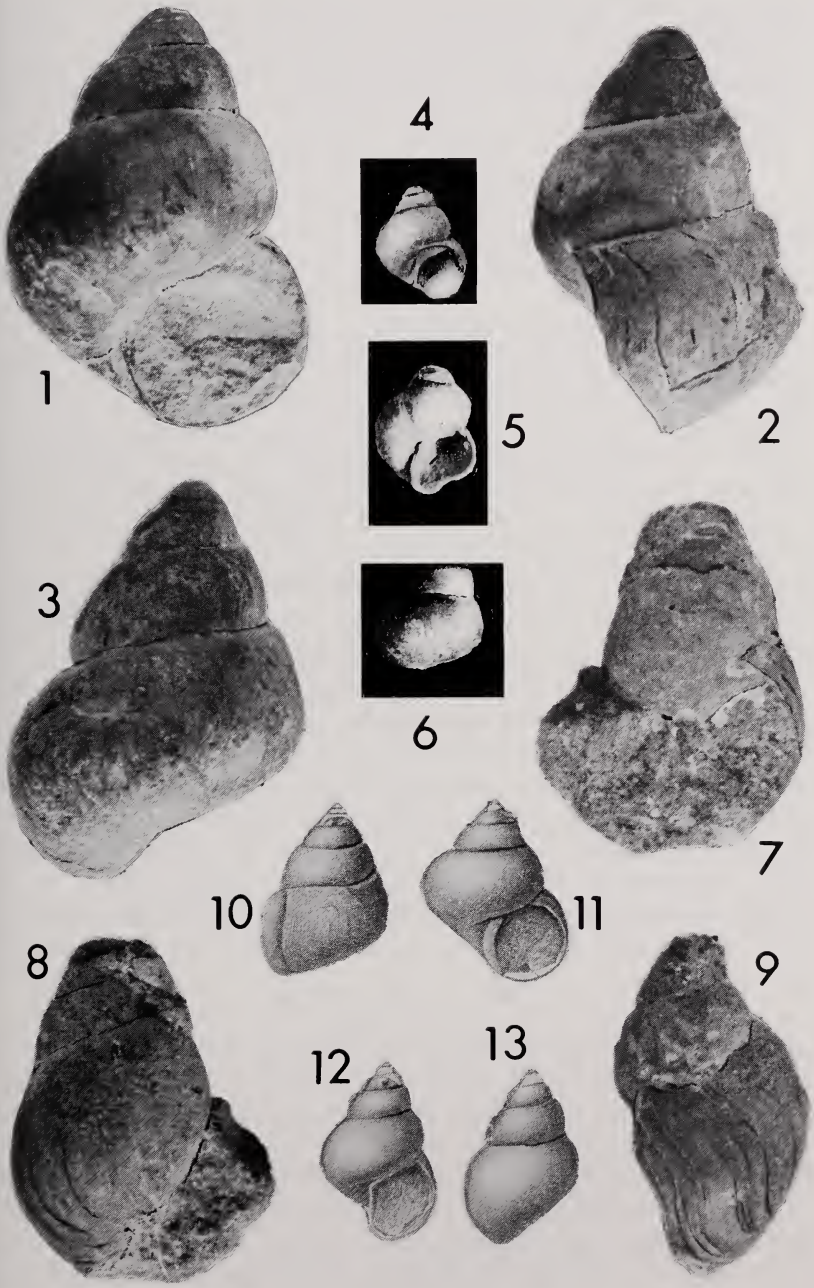
Vivipara (Paludina) lacerdae Hartt, 1870: 350.

Lioplacodes lacerdae, White, 1887:234, pl. 26, figs. 19, 20.

DESCRIPTION: "Shell rudely subovate, spire conical; volutions 4 or 5 in number, strongly and regularly convex; suture deeply impressed; the last volution regularly convex from suture to umbilicum, which is rimate; surface marked by lines of growth which, near the aperture of adults, are stronger, and show the border of the outer lip to have been sinuous; aperture subcircular. Length 16 millimeters; breadth of the last volution [D.] 13 millimeters." (White).

PLATE 12

1-3. *Lioplacodes feruglioi* Parodiz. Type, x1¾.
4-6. *Lioplacodes wichmanni* Doello-Jurado. Type, x1.
7-9. *Paleoanculosa bullia* (Ihering). (Type of *Melania pehuenchensis* Doello-Jurado) x1½.
10,11. *Lioplacodes lacerdae* (Hartt). Type, x1.
12-13. *Lioplacodes williamsi* (Hartt). Type, x1.


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According to the original illustrations, the outer lip seems to be very thick and folded, and the suture very deep. Otherwise it is much like *Viviparus*.

TYPE LOCALITY: Monserrate, 10 km. N. of Bahia, Brazil. The age, first indicated as Cretaceous (Mastrichtian), is in all probability Paleocene. Type probably in MNRJ.

?*Lioplacodes williamsi* (Hartt) 1870

Plate 12. figs. 12, 13

Vivipara (Paludina) williamsi Hartt, 1870: 351.
Lioplacodes williamsi, White, 1887: 235, pl. 26, figs. 21, 22.

DESCRIPTION: "Shell subovate or subconical; spire moderately extended; volutions about 5, regularly convex; suture deeply impressed; umbilicus rimate; aperture subovate, somewhat prominent anteriorly; surface marked by the ordinary lines of growth which show the margin of the outer lip to have been sinuous. Length 15 mm., breadth [D.] of the last volution 10 mm." (White)

It has a more elongated shell than *Lioplacodes lacerdae* and shows greater similarity to *L. cretaceous* (Stanton) from the Cretaceous of Wyoming.

TYPE LOCALITY: Same as *L. lacerdae*. Type in MNRJ.

Lioplacodes **bolivianus,** new name

Paludina cf. *fluviorum* Sowerby, Fritzsche, 1924:22, pl. 2, fig. 4.

This species is know only from a cast figured by Fritzsche which is that of a *Lioplacodes*, 22.5 mm. long, with the larger diameter in the body whorl of 12 mm. The last whorl occupies about half the total length. It has 4 whorls separated by a well marked suture, as in *Lioplacodes lacerdae*. The cast shows faint indications of spiral lines on the body whorl. It is the largest of the South American species of this genus. The name *fluviorum* was given by Sowerby to European fossils of the genus *Paludina* (1837, Min. Conchol.,: pl. 22, figs. 1-13).

TYPE LOCALITY: Comon, Potosí, Bolivia, in the Miraflores limestone of Upper Puca, Paleocene. Type in NR?

Family AMPULLARIIDAE

The South American stock of this family is formed by the genera *Ampullarius, Marisa,* and *Asolene,* differentiated from those "ampullarias" of Africa and Asia which belong primarily to *Pila,* and to *Saulea, Afropomus,* and *Lanistes.* The oldest *Ampullarius* known are from the Oligocene of South America and the Pliocene of North America. *Lanistes* is recorded from the Eocene-Oligocene of Africa. Other records include *Saulea* from the Pleistocene of Uganda and the extinct genus *Kwangsispira* from the Pliocene of southern China. In the Recent

fauna of the northern hemisphere the Ampullariidae are known only from the southern United States. *Ampullarius* is well distributed in South America, but *Asolene* has subgenera of great regional endemism: *Felipponea* and *Pomella* in Uruguay, and *Surinamia* in Dutch Guiana. Although these may be considered rather primitive they are not known as fossils except in alluvial deposits of the very late Pleistocene, where *Ampullarius* is also abundant. The origin of the family is obscure. It may be related to the Viviparidae, and the similarities among Old and New World genera could be a case of parallelism.

Genus *Ampullarius* Montfort, 1810

Type: *Nerita urceus* Müller

= *Ampullaria* Lamarck, 1801 (not *Ampullaria* Lamarck, 1799 = *Pila*).
Pomacea Perry, 1811.
Conchylium Cuvier, 1816.
Pomus H. & H. Adams, 1856.

Lamarck in 1799 used the name *Ampullaria* for *"Helix ampullacea"* Linnaeus. The identity of the species *H. ampullacea* was questioned by early authors because the specimen under that name in the Linnaeus collection did not agree with the description in the "Systema Nature" or the "Museum Ulricae." Also Linnaeus indicated "habitat in Asia" for *H. ampullacea,* although the true type locality was unknown. To the name *Ampullaria ampullacea,* Lamarck (1799) added "Cordon Bleu" (a common name given by d'Argenville to an Indonesian species). Other early indications of types for Lamarck's *Ampullaria* were: *A. rugosa* = *Nerita urceus Müller* (by Lamarck himself in 1801); and *A. guayanensis,* by Children (1823). Meanwhile, Montfort in 1810 had named the genus *Ampullarius,* with the same type as Lamarck's 1801, *Nerita urceus.*

In 1923, the International Commission on Zoological Nomenclature declared valid the names in the "Museum Boltenianum" published by Röding in 1798, and by such rule *Pila* gained a year's priority over *Ampullaria.* The second species listed under *Pila* (*"Der Ball,"* page 145 of Bolten's catalogue) included *P. equestris* as equal to "Gmel. Helix ampullacea." Thus, *Ampullaria* Lamarck became a synonym of *Pila,* containing the Old World species. For the South American species, the oldest generic name available was *Ampullarius* Montfort with the same type as Lamarck's second designation.

Subgenus *Limnopomus* Dall, 1904
Type: *Ampullaria columellaris* Gould

Ampullarius (Limnopomus) manco (Pilsbry)
Pomacea manco Pilsbry, 1944:145, pl. 11, figs. 31, 32.

This is a species of very small size. The contour of the shell cast agrees with *Limnopomus,* and is also somewhat similar to *Asolene* but lacks the expansion of the lip. Pilsbry's short description follows:

"The shell internal cast is globular, umbilicate, with a moderately elevated spire. The last whorl is evenly convex. The aperture is semilunar, rather narrow. L. 15.5 mm., D. 14.5 mm.; another specimen D. 16 mm."

TYPE LOCALITY: Quebrada Sungarillo, in strata with *Hemisinus paleus,* Oligocene, at the Pachitea River, Colombia. Type in ANSP.

Superfamily VALVATACEA
Family VALVATIDAE
Genus *Valvata* Müller, 1774
Type: *Valvata crispata* Müller

These fresh-water Mesogastropoda are typical of the northern hemisphere, entirely absent in the Recent fauna of South America. Fritzsche (1924) described some fossil species from the Argentina-Bolivia frontier region found in the upper strata of the Puca formation (Miraflorian), Paleocene. The fossils were badly preserved and the illustrations do not show clear distinctions among them. The species are (generic identification still doubtful):

Valvata yaviana Fritzsche, 1924:23, pl. 2, fig. 7. Yaví, W. of La Quiaca, province of Jujuy, Argentina.

Valvata satira Fritzsche, 1924:24, pl. 2, fig. 8. Same loc. as *yaviana.*

Valvata humilis Fritzsche, 1924:24, pl. 2, fig. 6. Miraflores, 17 km. N. of Potosí, Bolivia. See also Ahlfeld, 1946:177, pl. 7, fig. 9.

The species I described as *Valvata windhauseni* (Parodiz 1961b:16, pl. 1, figs. 1-6) from the Paleocene of Patagonia is, in my present opinion, and after comparison with other fossils, a representative of the genus *Potamolithus* (see page 114).

The types from the Steinmann collection are in the NR.

Superfamily RISSOACEA
Family HYBROBIIDAE (= ?TRUNCATELLIDAE)

The family name for the "Hydrobias" and allied genera has been a subject of long-lasting controversy. For convenience, most authors have

been using the name Hydrobiidae which includes several subfamilies (Hydrobiinae, Littoridininae, Amnicolinae, Lithoglyphinae). Pilsbry at different times used Hydrobiidae or Amnicolidae. The International Commission on Zoological Nomenclature ruled (opinion 457) in 1957 that Bithyniidae Gray, 1857 (original Bithynia-dae), should be placed in the approved list of family names, against Hydrobiidae or any of the other names. This decision failed to satisfy the specialists, most of them regarding Bulimidae (= Bithyniidae) as a family well separated from the "Hydrobias." H. B. Baker (1960:34) advanced a well-supported opinion that Truncatellidae Gray, 1840, has precedence, but that if *Truncatella* Risso, 1826, is to be excluded from that family (Thiele, 1929, included Truncatellinae-Pomatiasinae in it), Hydrobiidae (Hydrobi-ae Troschel, 1857) "would become the legal name for the restricted family" (Baker). The subfamily Hydrobiinae, comprising genera of the northern hemisphere, are absent in South America, although in many original descriptions of species in geological works, the *Littoridina* were referred to *Hydrobia.* But some species indicated as *Hydrobia,* for example *Hydrobia dubia* Etheridge (Pleistocene of Acre, Brazil), evidently do not belong to this genus.

Subfamily LITTORIDININAE (Note 49)
Genus *Potamolithus* Pilsbry, 1896[1]
Type: *Potamolithus rushi* Pilsbry

= *Paludestrina* (in part) d'Orbigny, 1840.
Lithoglyphus (in part) of authors.

Potamolithus was regarded by Pilsbry (1911) as belonging to the stock of early non-marine mollusks of Gondwana or pre-Gondwana origin. If this origin is supported on account of its likeness to the African genus *Lobogenes,* then all other relationships which it shows with groups of the northern hemisphere are left without explanation. On the other hand, the fossils here referred are from areas, or from an age, not belonging to that southern single mass of land that forms the Gondwana concept.

Different from the Thiaridae, Pleuroceridae, Viviparidae, Hyriiadae, and other fresh-water families that entered the southern hemisphere at the very end of Cretaceous time, known examples of the early Tertiary *Potamolithus* are very scarce. It may be an authochtonous group. In the Recent fauna the genus is geographically restricted, parallel to


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that of *Neocorbicula,* to the Paraná-Uruguay river system. For their origins, there are three possible alternatives:

1. The group is very ancient, cosmopolitan, and probably derived from an ancestral stock in Gondwana.

2. The genus is of northern ancestry and migrated into South America at the end of the Mesozoic.

3. It is a relatively modern group, derived directly from marine ancestors.

Of these, No. 3 is the most acceptable on the basis of the fossil record.

1 For complete discussion of this genus see Parodiz, 1965.

The Neartic genus *Pilsbryus* from the Idaho formation, Pliocene of North America (related to *Lithoglyphus* and *Flumunicola*), resembles *Potamolithus.* The latter is probably also related to *Tropidebora,* from the Pebas formation, Pliocene, of Peru. Contrasting with *Littoridina,* whose fossils are so abundant in the Pleistocene deposits of South America, *Potamolithus,* after its first appearance in the Paleocene, is found again only in the Recent.

Potamolithus capitatus (Mayer-Eymar), 1900
Plate 13, figs. 5, 6

Bythinia (Assiminea) capitata Mayer-Eymar, in Burckhardt, 1900: 24, pl. 26, figs. 12-14.
Potamolithus capitatus, Parodiz, 1965:18.

ORIGINAL DIAGNOSIS: *"Testa conica, apice acuta. Anfractus sex, convexi, velociter increscentis, sutura profunda separatis, longitudinaliter striati, ultimus majusculum. Long.* 5, *Lat.* [diam.] 3 mm.".

TYPE LOCALITY: East of Pacunto, western slope of the Bío-Bío Valley, Chile. In sandstone (lower Eocene) with *Diplodon burckhardti* and *Ancylus humboldti* Mayer-Eymar. It is very abundant and in certain parts the sandstone contains shells of three different sizes, but undoubtedly of the same species. The typical ones are those resembling *Bithynia* with more elongated spire. The type is probably with the Mayer-Eymar collection in Zurich.

According to Burckhardt and other geologists of his time, the upper Bío-Bío zone strata were lowermost Eocene, but it is more likely that

MAP 4

– – – – – Western distributional limit of living *Potamolithus.* Fossil locality 1., Paleocene.

——— Western distributional limit of living *Neocorbicula.* Fossil localities: 2. Paleocene. 3. Eocene. 4. Miocene. 5. Pliocene.

Arrows indicate directions of migration during middle Tertiary.

they represent lower Concepción, as an equivalent of the Jahuel formation of Patagonia (Note 45). Frenguelli, who on several occasions explored the region, indicated (1940) that "the oldest horizon from the Riochican up of Aguada del Guanaco in Neuquén, contains at their base strata with numerous fresh-water mollusks (*Amnicola, Chilina, Diplodon*) which filled some lacustrine areas in older eroded rocks." Again in 1941, the same author referred to fossil "*Bythinia*" at the base of the Tertiary tuffs in the province of Neuquén (on the road to Sierra Miranda), which he identified as pertaining to *Potamolithus*, "probably the same of the Chilean territory determined by Mayer-Eymar as *B. capitata*." Finally, reaching the Arroyo Pedregoso in the Bío-Bío valley near the site indicated by Burckhardt, Frenguelli (1941) also found "*Unio, Actaeonina* and *Bythinia*" which "corresponds as the lacustrine Tertiary of Aguada del Guanaco and Sierra Miranda, to the genera *Diplodon, Chilina* and *Potamolithus*."

These findings were confirmed by Feruglio (1949, 1:134) who collected, at Laguna del Molino (southern border of Gran Bajo de San Julian) in Santa Cruz, "a small gastropod like a *Valvata*, but without open umbilicus and rather referable to the Hydrobiidae of the genus *Potamolithus* or a very close one." The age indicated in this case was "older than Cretaceous," which is very doubtful. The specimen probably belongs to the same early Tertiary age indicated by Frenguelli.

Our specimens at hand of *P. capitatus* are somewhat distorted by diastrophic pressure, but one of them, better preserved, shows a submarginated suture, recalling the living species *P. rushi* Pilsbry. It is from the "Terciario Carbonifero" of Concepción, Chile, and was collected by Dr. Fuenzalida in 1941 together with *Neocorbicula* and *Paleoanculosa*.

Only one isolated species living in Chile, *P. australis* Biese, shows closer resemblances to those of the Paraná-Uruguay basin.

?*Potamolithus windhauseni* (Parodiz)

Valvata windhauseni Parodiz, 1961b:16, pl. 1, figs. 1-6.

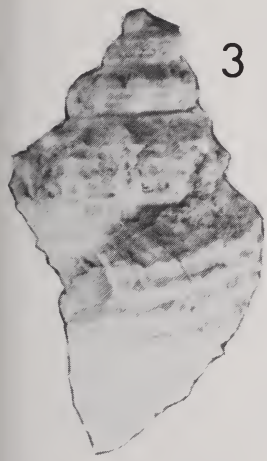
DESCRIPTION: Shell with almost five whorls (the last portion of the body whorl not completely preserved), increasing regularly and very convex but at the peri-

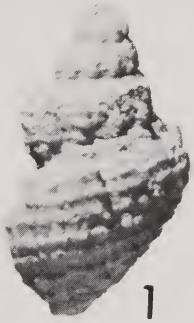
PLATE 13

1-4. *Pyrgulifera sehuena* Parodiz. 1. Type, x1½; 2. Paratype, x1½; 3, 4. Paratypes, x2½

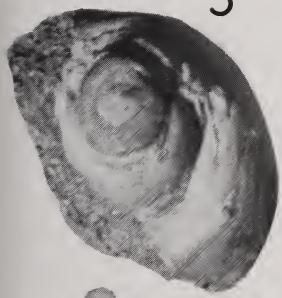
5,6. *Potamolithus capitatus* (Mayer- Eymar). x4.

7-9. *Potamides chaliana* Parodiz. 7, 8. Type, x2; 9. Paratype, x2.

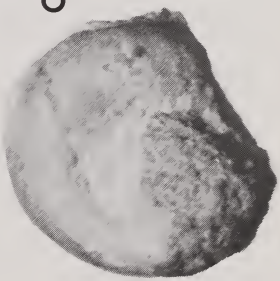

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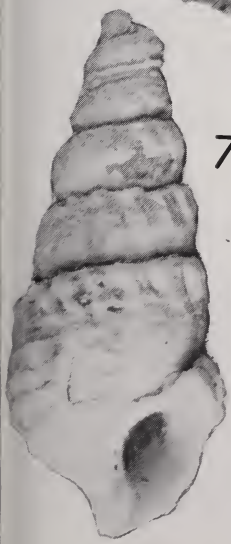

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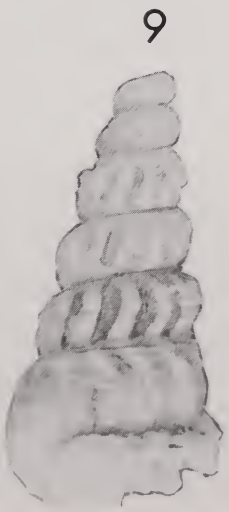

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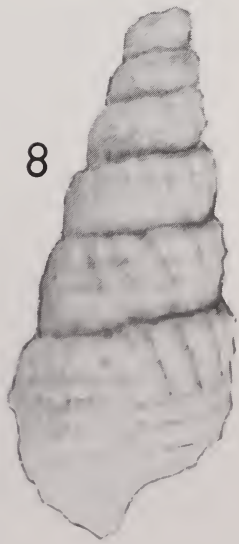

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phery of last whorl shows a marked angulosity with a carina or marginated keel. The carina starts at the end of the suture, above the apertural angle; below it the whorl is convex again. The best-preserved portion of the last two whorls is conspicuously marked with regularly spaced oblique striae (interspaces about 0.4 mm.) that are also visible at the base. It has a wide umbilicus, although the area is partially covered with the hard calcareous matrix. The altitude of the last whorl from suture to keel is about equal to the rest of the spire, and the whole shell is almost as high as wide. The apex, well preserved, is obtuse.

DIMENSIONS: Height 6 mm., major diameter 8.5 mm., length from apex to carina 4.5 mm., lesser diameter 7.5 mm.

TYPE LOCALITY: Nahuel Niyeu, 25 miles W. of Valcheta, province of Río Negro, Argentina, in lacustrine deposits of the Jahuel formation, Paleocene. Collected by R. Wichmann, 1923. Type in CM.

Of four paratypes the smallest is a well-preserved inner cast, crystallized by infiltration of silica, a characteristic of many of the fresh-water fossils found in these strata. The silification is also present in the holotype apex. The other paratypes are longer than the holotype, and clearly show the carina, filled with tuffaceous matrix and deformed by pressure due to the strong diastrophism which subsequent to deposition affected the sediments during the Tertiary.

The same strata contain *Diplodon bondenbenderi, Physa wichmanni, Lioplacodes,* and other fresh-water shells.

Genus *Potamolithoides* Marshall & Bowles, 1932
Type: *P. biblianus* Marshall & Bowles

The characteristics of this genus are implied in the description of its monotype, emphasizing the small size, depressed spire, and excavate-umbilicated base. The authors rendered it closer to *Potamolithus,* but it also may be related to *Lithoccocus,* a genus now living in the same area. (See Note 48.)

Potamolithoides biblianus Marshall & Bowles, 1932:4, pl. 1, figs. 1-3
Plate 17, figs. 1, 2

ORIGINAL DESCRIPTION: "Shell small, somewhat beehive form. Apical whorls depressed, planorbiform, the embryonic whorl slightly sunken. Whorls rapidly increasing, flattish on the upper surface, body whorl large, subangular at the periphery, sutures linear. Base flat, widely umbilicate (or deeply excavate). Aperture oblique, outer lip thin, basal lip sinuate. Parietal wall with a thick, upstanding callus which makes the peritreme continuous. H. 3.5 mm., greater d. 5 mm. Largest paratype, H. 5 mm., g. d. 7 mm."

TYPE LOCALITY: Biblian, province of Canar, Ecuador, middle Miocene, found in same strata with *Poteria bibliana, Doryssa,* and *Diplodon.* Type in USNM.

Genus *Lyrodes* Doering, 1885
Type: *L. guaranitica* Doering

=*Potamopyrgus* (in part) of authors.
Pyrgophorus Ancey, 1888.

Lyrodes has been used as a synonym of *Potamopyrgus* Stimpson. In 1939 Morrison described the differences between these two genera, of the Neotropical region and New Zealand respectively. The status of *Lyrodes* was finally stated by Pilsbry in 1944. Taylor (1966:190) suggested relationship with *Tryonia,* but *Lyrodes* is more similar to those North American Pliocene and Pleistocene genera *Calipyrgula* and *Durangonella* (comparing *L. guaranitica* with *C. carinifera* Pilsbry). Although not abundant in species, the genus has a large distribution from Venezuela to Argentina — apparently absent in the southwest — and also in Cuba. The oldest fossil record is from the Oligocene of Colombia, and probably the group expanded northward in the Pliocene, evolving into new generic forms. The original description by Doering is as follows (translation):

"Shell subperforate, elongated, oval-conic, thin, transluscent, carinate, setaceous, with spiral lines. Animal with oblong foot lyre-shaped (hence its name), with two retractile anterior lobes and lanceolate posteriorly; tentacles subconis, baculiform [rod-shaped] rostrum short." The neotype of *L. guaranitica* (see Parodiz, 1960:24) is from Arroyo Riachuelo, near Corrientes city, Argentina.

Lyrodes laciranus (Pilsbry & Olsson)
Plate 16, fig. 4

Potamopyrgus laciranus Pilsbry & Olsson, 1935:9, pl. 5, f. 6.

ORIGINAL DESCRIPTION: "Shell small, whitish, elongated conic, the spire generally 3 to 4 times the length of the aperture. Whorls about 6, moderately convex between deep sutures. Nuclear whorls small, not well showing on any of our specimens. Surface smooth, porcelaneous, generally with 3 to 5 fine, raised spiral threads, their intervals wider and unequal, on the middle and lower half of each whorl, the sutural band above being generally smooth. Aperture broadly ovate, outer lip thin. L. 4 mm., D. 1.7 mm.; 6 whorls."

TYPE LOCALITY: Near Zopffs, in hematitic sandstone of La Cira formation, Middle Magdalena Valley, Colombia, Oligocene. Very abundant in many localities near La Cira. Type in ANSP.

L. laciranus belongs to that group of little- or not-carinated species (some specimens according to Pilsbry appear slightly carinated) with

very variable sculpture, resembling the living *L. doellojuradoi* Parodiz. But *L. laciranus* is shorter and the revolving lines are ordinarily well marked.

I wish to take this opportunity to clarify the status of *Lyrodes scotti delticola* Doello-Jurado. Since publication of my paper of 1960, I have observed the types of that form at the Buenos Aires Museum, and conclude that they do not represent a subspecies of *L. scotti* but are typical specimens of *L. guaranitica*. These are from the Pleistocene of the Buenos Aires province.

Genus *Dyris* Conrad, 1871
Type: *Dyris gracilis* Conrad

Conrad, 1871:195.
=*Isaea* Conrad, 1871 (not Edwards, 1830).
Conradia Wenz, 1925 (not A. Adams, 1860).

This is an extinct genus, allied to *Calipyrgula* and *Lyrodes,* briefly diagnosed by Conrad as "Subulate, with many volutions, aperture ovate, labium reflexed." Five specific names were included in *Dyris,* from the Peru-Brazil border region, and especially from the Pebas formation, Pliocene, of northeastern Peru:

Dyris gracilis Conrad, 1871:195, pl. 10, fig. 8.

Dyris confusa (Boettger), 1878:491, pl. 13, figs. 4-7. Originally described as *Hydrobia (Isaea).*

Dyris ortoni (Gabb), 1869:198, pl. 16, fig. 3. Originally as *Mesalia,* Turritellidae (and *Isaea* Conrad).

Dyris tricarinata (Boettger), 1871:492, pl. 13, figs. 10, 11. Originally as *Isaea.*

Dyris lintea (Conrad), 1871:193, pl. 10, fig. 6. Originally *Isaea.*

Although *D. lintea* (Conrad) had page precedence over *D. gracilis,* the former species was under the preoccupied *Isaea,* which leaves *gracilis* as the first species mentioned by Conrad under *Dyris.*

The variations in these "species" are so numerous and intergrading that practically, only two different species can be recognized:

Dyris ortoni (Gabb) = *confusa* Gabb.

Dyris gracilis Conrad = *tricarinata* Boettger, = *lintea* (Conrad).

The larger, *D. ortoni,* has little or no sculpture, and it is more like *Littoridina. D. gracilis* comprises forms with many spiral cords, widely

variable, with a tendency to concentration of the cords on the middle line above the suture (these are the *D. tricarinata* and *D. lintea*). In a lot from the Javary River, near Tres Unidos, Peru, I have observed the clinal transition among the three forms. The same variations can be observed in the numerous specimens illustrated by de Greve (1938, pls. I and III). This author gave extensive descriptions of the five nominal species and their variations (under "*Hydrobia-Conradia*").

Individual forms of the same species and of the same stratigraphic units may belong to different generations, perhaps separated by time considerably longer than can be observed in Recent species. Such separation, with sharp variations among generations, may have led early paleontologists to consider them as different species.

It must be added that only those fossils collected in the vicinity of Iquitos, Peru, belong to the Pliocene Pebas formation. Others, mentioned from western Brazil by Oliveira Roxo and other authors, are of Pleistocene, not Pebasian, age. Pebas formation, as such, does not occur in Brazil (see G. G. Simpson 1961; also Note 19).

The types of *D. gracilis* and *D. lintea* are in the ANSP.

Genus *Liris* Conrad, 1871

Type: *Liris laqueata* Conrad

Conrad, 1871:194.

This genus is poorly known and somewhat neglected in the malacological and paleontological literature. After Conrad, the only mention and description of *Liris* (as well as *Dyris*) species, was that of de Greve (1938). The latter author placed *Dyris* in Rissoidae and *Liris* in "Melaniidae," which was also Conrad's assumption. More acceptable is Wenz's inclusion of both genera in Hydrobiidae (Littoridininae), closer to *Lyrodes*, but the correct systematic position remains unsettled.

Liris and *Dyris* occupy the same ecological niche in the transitional period between Pliocene and Pleistocene. Typical *Liris* members differ from those of *Dyris* by having strong axial ribs instead of spiral cords, but in *L. tuberculata*, a combination of these two types of sculpture exists. This species belongs to *Liris* on account of its apertural features (the peristome detached from the wall of the body whorl). Conrad's original diagnosis defines *Liris* as "Elongated, subcylindrical, with convex whorls and oblique longitudinal ribs; aperture suboval, small, peristome continuous, labium reflexed and prominent." Only three species are known:

Liris laqueata Conrad, 1871:194, pl. 10, fig. 3. De Greve, 1938: 89, pl. 2, figs. 10, 14, 31; pl. 6, fig. 11.

The original illustration is so small that details are not discernible, but de Greve provided a good series of photographs. This species differs from *L. minuscula* by its weaker axial ribs, proportionally slender shell, and its peristome extending free into a tubular shape, in the manner of a *Clausilia* (this feature is very variable). The type is in the ANSP.

Liris minuscula (Gabb)

Turbonilla minuscula Gabb, 1869: 197, pl. 16, fig. 1.
Liris minuscula, de Greve, 1938: 92, pl. 1, figs. 31-35, pl. 2, figs. 1, 9, 11, 13; text figs. 12-18.

This species has stronger ribs beginning at a deep suture, giving to that line a festoon-like appearance, but the development of the ribs varies considerably. The body whorl usually is wider than in *L. laqueata*. According to de Greve the embryonic whorls are angulate-carinate with many oblique axial riblets. In spite of its name it is generally larger than *L. laqueata*.

Liris tuberculata de Greve, 1938:96, pl. 2, figs. 32-35; pl. 3, figs. 1-20; text figs. 19-22.

This species is characterized by the combination of the axial ribs, as in *L. laqueata*, with spiral cords, as in *Dyris*. On each whorl, the upper spiral cord forms a carina, with the upper surface of the whorl convex. It is the largest species in size.

The average sizes of the three species are:
L. laqueata 3.7 mm. x 1.9 mm. Type in ANSP.
L. minuscula 4.9 mm. x 1.6 mm. Type in ANSP.
L. tuberculata 5.1 mm. x 2.0 mm. Type in ZIUZ.

The typical locality for *L. laqueata* and *L. minuscula* in Conrad and Gabb was Pebas. The materials collected by B. Peyer and studied by de Greve were from the Itayu River, in the same Iquitos region of Peru.

Genus *Toxosoma* Conrad, 1874a

Toxosoma Conrad, 1874a:31 Type: *T. eborea* Conrad
= *Pseudolacuna* Boettger, 1878

The systematic position of this extinct genus is problematic. Pilsbry (1944:151) thought that it was related to *Ebora* "in the Amnicolidae" (*Ebora* Conrad, 1871, not Walk, 1867, should be placed according to

Wenz in *Pseudocirssope* Boettger, 1906, a subgenus of *Lacuna*). Conrad's type was not properly recognized, so Etheridge, de Greve, and Wenz referred the species to *Pseudolacuna macroptera* Boettger, which Pilsbry indicated as a synonym of *T. eborea*. If Pilsbry's opinion about the relationship of *Toxosoma* with *Ebora* is confirmed, then *Pseudocirssope* should be removed from Lacunidae.

The outline and proportions of *Toxosoma* are like a very elongated *Potamolithus*, although the two are probably not related. The most remarkable feature of *Toxosoma* is the very thick callus on the columella, with a strong tooth-like fold placed deeply on the columellar wall, not distinct from a front view but conspicuous when the aperture is viewed obliquely. It also has a channeled base. The smooth surface is ivory-like.

Toxosoma eborea Conrad

Conrad, 1874a:31, pl. 1, fig. 7. Pilsbry, 1944:151, fig. 3a, b *(eboreum)*. *Pseudolacuna macroptera* Boettger, 1878:416, pl. 3, figs. 14-15. De Greve, 1938:74, pl. 15, figs. 17, 18, 24, 29, 31, 36.

Pilsbry gave the following complementary description of this species: "The shell is imperforate but has a long, impressed umbilical suture. Surface smooth, faintly showing a few slight lines of growth of a reversed sigmoid shape. The spire is straightly conic, the apex somewhat obtuse, the whorls rather strongly convex. There are barely six whorls, the first one scarcely descending, not showing in a face view. The last whorl is very well rounded, but in its last third becomes compressed laterally near the base, and flattened on the umbilical side. The outer lip is broken away. The columellar lip is reflexed in the middle part, which is seen to be rather deeply concave in lateral view, continuous with the thick, raised parietal callus. Columella concave. In an oblique view in the mouth the lower end of a strong columellar fold is seen on the upper part of the columella. L. 4.7 mm."

The width of the shell, according to Boettger, is 4 mm., with an aperture 1.5 mm. x 2.5 mm. De Greve specimens measured 3 mm.-3.7 mm. in length, and in aperture 1.8 mm.-2.3 mm. x 1.2 mm.-1.3 mm. The figures given by this author show many variations in length of spire, development of outer lip, and columellar fold.

TYPE LOCALITY: Pebas, Iquitos, Peru, in the Pliocene Pebas formation. Type in ANSP.

Subfamily ?NYMPHOPHILINAE Taylor
Genus *Tropidebora* Pilsbry, 1944

Type: *Pachytoma tertiana* Conrad.

Tropidebora tertiana (Conrad)
Pachytoma tertiana Conrad, 1874a: 31, pl. 1, fig. 11.
?*Helicina tertiana*, de Greve, 1938:68, pl. 4, figs. 26-28, 31.
Tropidebora tertiana, Pilsbry, 1944: 150, fig. 2.

Creating this genus Pilsbry figured Conrad's type, as probably related to *Potamolithus*, especially *P. felipponei* Pilsbry from Uruguay. The species was redefined as follows: "Two whorls following the apical whorls have a low carina in the middle of the upper surface as well as a peripheral keel concealed in the suture. On the last whorl the upper carina is wanting. The outer lip is expanded, its face flattened, with a raised inner rim. There is a flattened area behind the rather thick columella, as in some species of *Potamolithus*. Diameter 5.8 mm.; 4½ whorls." The type is in ANSP.

TYPE LOCALITY: Pebas formation, Pliocene, Iquitos region, Peru.

Nymphophilus Taylor (1966:199), a recently described living genus from Cuatro Ciénagas, Coahuila, Mexico, has extraordinary resemblance to *Tropidebora*. I have observed several hundred specimens of the type species, *N. minckleyi* Taylor, collected by C. J. McCoy in 1966. Perhaps the Mexican isolated living form is the result of late Pliocene or Pleistocene migration northwards. In the locality of Cuatro Ciénagas the remarkable gastropod fauna described by Taylor shows great affinities with that of the Pebas formation.

The relationship *Tropidebora-Potamolithus* assumed by Pilsbry cannot be proved by the fossils, but *Nymphophilus* suggests a notable difference in the structure of the copulatory organ. For that reason I include, provisorily, *Tropidebora* with the *Nymphophilinae*.

Superfamily CERITHIACEA
Family PLEUROCERIDAE

Most recent and fossil Pleuroceridae in South America are representatives of the genera *Pachychilus* and *Doryssa*. These are more abundant in the northern, warmer region. Only *Doryssa* (a few species) advanced as far south as the Paraguay-Parana system, never reaching La Plata River. Fossils are abundant in southern strata, especially of Patagonia where during the early Tertiary the climate was more favor-

able. In 1887 Philippi described a "*Paludina araucana*" which corresponds — according to new materials collected by Fuenzalida at Concepción, Chile — to the new genus *Paleoanculosa*. Fritzsche in 1924 named *Melanoides bicarinata* a *Pachychilus* from northwestern Argentina, and Pilsbry in 1939 described *Doryssa* from Bolivia. Both forms are Paleocene.

The anatomy of the living Pleuroceridae indicates that they are close to the Cerithiidae, and differ from the Thiaridae (both were formerly included in the "Melaniidae" complex), by being dioceous, not parthenogenetic, the female having an egg-lying sinus on the right side of the foot. The North and South American genera belong to the subfamily Pleurocerinae, and the classification adopted is that of Morrison, 1954:

NORTH AMERICA	SOUTH AMERICA
Oxytrema	*Pachychilus*
Subgenus *Strephobasis*	Subgenera *Oxymelania*
Gyrotoma	*Glyptomelania*
Mudalia	*Pilsbrychilus*
Subgenus *Leptoxis*	
Eurycaelon	*Doryssa*
Pleurocera	
Subgenus *Ellipstoma*	*Paleoanculosa* (extinct)
Io	

Paleoanculosa, new genus

This generic group bears similarities to the living North American subquadrate species of Pleuroceridae. The shells of *Paleoanculosa* have a large body whorl with short spire and columella thickened by heavy callus. The body whorl is depressed above the middle line and the whorls are subgradate or shouldered. The surface is marked with waving lines of growth. The outline has a certain resemblance to *Gyrotoma*, lacking the sinus on the upper apertural angle, and also recalls some species of "*Anculosa*" (antedated by *Leptoxis* according to Pilsbry, Morrison, and Parodiz) from the Coosa River of Alabama, for example, *A. taeniata* Anthony. In other features it may be compared with *Strephobasis*. It is clear that morphological differences from these living groups, as well as age and geographical separation of *Paleoanculosa*, justify its new generic name. Doello-Jurado (1927:414) was the first to suggest that his "melanians" were "probably of an extinct genus." Compared with fossils of the Old World, some individ-

uals of *Paleoanculosa* look slightly like members of *Tulotomoides* from the Pliocene of China. The latter genus, according to Wenz, belongs to the Viviparidae.

Paleoanculosa is found only in the Paleocene of southern South America (extending perhaps into the lower Eocene). Its type is the following species:

Paleoanculosa patagonica, new species
Plate 14, figs. 3,4.

DESCRIPTION: Shell large and solid, almost subquadrate, with the upper whorls slightly convex. Body whorl large, about four-fifths of the total length, with a weak shoulder below which the wall of the whorl is compressed, corresponding to the inner curvature of the sigmoid growth lines (as in *Anculosa*); inferior portion decidedly convex. Aperture oval, angulated above and rounded at the base. Columella with a heavy callus about 1.5 mm. thick. Suture well marked and irregular but not excavated. Lines of growth conspiciously sinuous. Very faint spiral lines are observable on the shoulder of the larger specimen. The shape has a remote resemblance to *Chilina* but, apart from other generic differences, the columella is not folded.

DIMENSIONS: The type is an almost complete specimen, but with the basal lip broken; length 24 mm., diameter 17.5 mm.; last whorl estimated at 19 mm. Three paratypes, two smaller and incomplete, and one larger, of 25 mm. x 19 mm. (body whorl only). Type is CM.

TYPE LOCALITY: Lenza Niyeu, NW. of Valcheta, province of Río Negro, Argentina, found in the same strata with *Lioplacodes feruglioi* of the Jahuel formation, Paleocene; collected by R. Wichmann, 1923.

The type specimen was examined by Doello-Jurado, who assigned it to his *Viviparus wichmanni* (1927:412), but indicated that the sinuosity of the striae of growth were not present in the specimens of that species from General Roca, adding that such character "might be a good criterion for future comparisons with congeneric fossil species from other continents." (p. 413)

Paleoanculosa macrochilinoides (Doello-Jurado)
Plate 14, fig. 5
Plate 15, fig. 11

Melania macrochilinoides Doello-Jurado, 1927: 416, pl. 11 (of Wichmann) fig. 75.

DESCRIPTION: Larger than *P. patagonica,* with more conical spire of six whorls (the first detached), and prominent shoulder. Growth lines very faintly marked and less sinuous than in *P. patagonica.* Below the shoulder, the body whorl is very inflated. The outer lip is not complete but shows that it must have been sigmoid.

The resemblance to *Macrochilina (=Solenoides)* indicated by its author is only remote.

DIMENSIONS: Type and only known specimen, length 38 mm., major diameter 19 mm., minor diameter 18 mm. The body whorl is about one-third of the total length.

TYPE LOCALITY: Doello-Jurado indicated the specimen was collected by Wichmann at Puente Rio Grande, Mendoza, but this is a mistake. It was collected by P. Groeber at Cerro Bayo de la Esperanza, province of Mendoza (see Groeber 1939b:74), and corresponds to the Jahuel formation, Paleocene. Groeber thought that the fossil could be of Barremian-Cenomanian age, but it was found in the same strata as the Paleocene *Diplodon*. Type in CM.

The general shape of *P. macrochilinoides* recalls that of *Hannatoma* from Peru, but that genus is one of the Thiaridae, typically tri-sulcated and with strong spiral sulcation or cords on the upper whorls.

Paleoanculosa bullia (Ihering)

Plate 12, figs. 7, 8, 9
Plate 14, fig. 2
Plate 15, figs. 2, 3 (type), 4, 6

Melania bullia Ihering, 1907b: 464, pl. 18, fig. 127. 1914:93.
Melania ameghiniana Doello-Jurado, 1927:413, pl. 10 (of Wichmann) figs. 61-71, pl. 11, fig. 74.
Melania pehuenchensis Doello-Jurado, 1927:415, fig. 77.

This species was based on a single specimen, the description of which was as follows (translation):

"Shell fusiform, imperforated, filled with the matrix, incomplete, lacking the anterior part of the aperture and the apex. Four whorls little convex, separated by a deep linear suture. The whorls ornamented by striae or fine spiral sulcations which appear especially on the posterior zone of each. The columella and wall of the aperture covered with a smooth lamella [callus] very thick. This shell comes from Rio Chico (Salamancan) and it was found with other marine [sic] shells. I am indebted to Dr. W. H. Dall who examined the specimen and whose opinion is that it corresponds to a *Melania*" (Ihering, p. 464).

Doello-Jurado, describing *M. ameghiniana*, stated that it lacks the callus on the columella. But Wichmann (1927:403) had already indicated the similarities of the specimens he collected to *M. bullia*. Wichmann materials from different localities of Río Negro include about 300 specimens (CM), which I revised recognizing the great variability of the form, from large and well-calloused specimens to smaller ones with waving lines of growth, one showing clear spiral lines, and others carinated at the base. Many specimens were decalcified because of

alteration of primary deposits before complete fossilization took place, and those "*in situ*" are mostly silicified. The geologist F. Pastore found many individuals "loose in the dunes marginal to the Barrancas River, at Mendoza" (see below).

Many complete and well-preserved specimens are from Bajo de Santa Rosa (found with *Diplodon*), a locality mentioned by Wichmann (1927:391). Others from the same locality were collected separately (figures 62 and 68 in Wichmann). The type of *M. ameghiniana* is from Aguada de Trapalcó, also collected by Wichmann. Both localities are in the Río Negro province. A large lot of 200 specimens, many in silicified fragments, was taken at Arroyo Trinetra, west of Nahuel Niyeu, and found also with *Diplodon* (Wichmann 1927:392), remains of turtles, fresh-water fish, and "*Chubutolithes,*" common in the Paleocene strata of the Jahuel formation.

TYPE LOCALITY: "Salamanqueen Río Chico, Chubut" as indicated by Ihering, corresponds to the same strata as those containing *Diplodon colhuapiensis*: northern Sehuenan in Chubut. Those of Río Negro are relatively older, from lower Jahuel, coeval with the Roca facies of San Jorge.

The single specimen (type in MACN) of *M. pehuenchensis* is also an individual of *P. bullia*. The aperture is filled with matrix but an uncovered portion of its superior angle shows the same calloused columella. The body whorl is not shouldered but rather flat, but with waving lines of growth very clear. It measures 26 mm. x 16 mm., and Doello-Jurado mentioned another, incomplete specimen (which I have not seen) reaching 30 mm. x 16 mm., from the confluence of the rivers Grande and Barrancas, Mendoza, collected by F. Pastore in 1912. The original type locality given for *M. pehuenchensis*, "Camul-có, south of Mendoza," was an error because the type is accompanied by a collector's label (Wichmann's) indicating Aguada de Trapalcó, where *P. bullia* is abundant. Wichmann, apparently, did not collect at Camul-có, and his reference to this locality was taken from Groeber. Furthermore *M. pehuenchensis* does not belong, as its name suggests, to the typical "Pehuenche" of Doering, which is Mastrichtian.

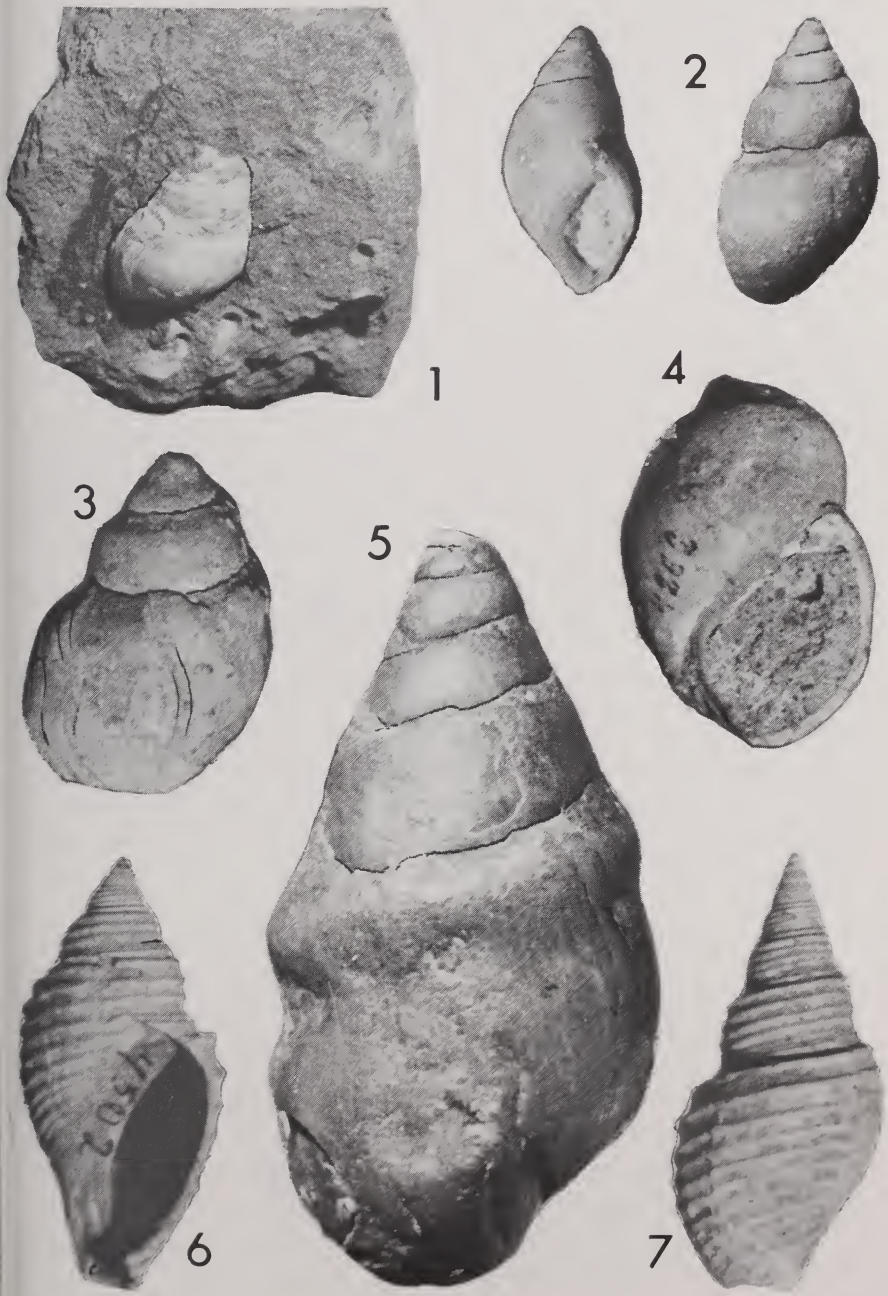
PLATE 14

1. *Paleoanculosa araucana* (Philippi), in sandstone of the "Terciario Carbonifero." x1.
2. *Paleoanculosa bullia* (Ihering). Ventral and dorsal views. x1½.

3,4. *Paleoanculosa patagonica* Parodiz. 3. Type, 4. Paratype, x1⅝.

5. *Paleoanculosa macrochilinoides* (Doello-Jurado). Type, x2½.

6,7. *Aylacostoma sulcatus* (Conrad). x2½.


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It might be that *P. bullia* represents a division of *Paleoanculosa* as indicated by its slender, less-shouldered, and more "bulimoid" form — especially when it is compared with *P. macrochilinoides* — but I hesitate to create a new subgeneric name for this single species.

?Paleoanculosa araucana (Philippi)

Paludina araucana Philippi, 1887: 74.

Philippi stated that this fossil belongs to "typical" *Paludina*, and the specimens which I am observing at present were described as such on the original label. However, in the old literature many fossils were placed under the names *Paludina* or *Melania* which belong elsewhere. The lot at hand was collected by H. Fuenzalida in 1941, in the "Terciario continental con mantos de carbón," between the marine Concepción formation (Eocene) above, and the marine strata of Boca-Levu (Danian) below. The age therefore must be Montian and equivalent to — or relatively younger than — Lonquimay (Note 45). The type locality of *Paleoanculosa araucana* was Punta Puchoco, coast of Concepción, in the "Carbón de Pucho."

The specimens observed (CM) are deformed by diastrophic lateral pressure, but in a general way seem to belong to a species very close to *Paleoanculosa patagonica*. One specimen still incrusted in the matrix offers a better comparison. It has the same gradate appearance, wavy lines and indications of a weak shoulder. The lignitiferous sandstone also contains remains of marine shells (*?Mytilus ramosus* Philippi) typical of the non-carboniferous Concepción formation. This indicates brackish-water conditions at the end of deposition of the fresh-water strata, in transitional Paleocene-Eocene time.

Subfamily POTADOMIINAE (=Melanatriinae)

Genus *Pachychilus* Lea, 1851

Type: *Melania laevissima* Sowerby (See Morrison, 1954).

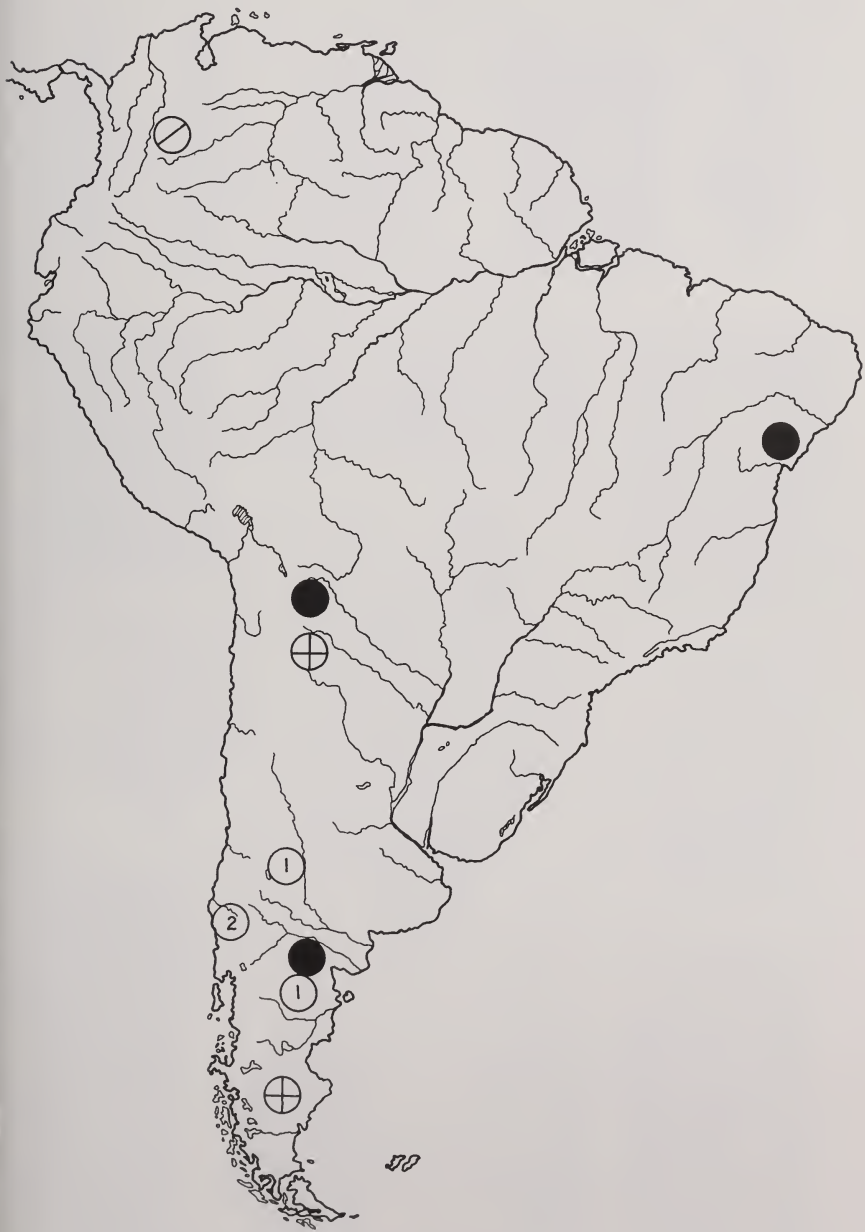
MAP 5

Genera extinct in South America.

● Paleocene *Lioplacodes*.

1., Paleocene, and 2., Eocene, *Paleoanculosa*.

⊕ Paleocene, and ⊘ Oligocene, *Pyrgulifera*.


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Pachychilus Lea, I. & H. C. Lea, 1851:179.
= *Pachycheilus* H. & A. Adams, 1857.
Cercimelania Fischer & Crosse, 1892.
Sphaeromelania Rovereto, 1899.

DESCRIPTION: This is the most common genus of Central and South American Pleuroceridae. Shells of medium-to-large size, elongate-conic outline, whorls slightly convex or completely flat, and without sculpture with the exception of very weak lines of growth.

Pachychilus (sensu lato) terebriformis (Morris)
Plate 15, fig. 1a, b

Melania terebriformis Morris, 1859:266, pl. 14, fig. 3a, b, c, Hartt, 1870: 350.
Melania nicolayana Hartt, 1870:350. White, 1887:238.
Pleurocera terebriformis White, 1887:236, pl. 26, figs. 10-13. Oliveira & Leonardos, 1943:575, 576.

REDESCRIPTION: Shell small, elongate, the sides of spire gently concave toward the apex and convex for the proximal half of the shell; volutions 8 or more, somewhat flattened at the outer side, the larger ones showing a slight constriction about their middle and a somewhat prominent rounding or shouldering of the distal border, adjacent to the suture. The last volution not inflated, gradually rounded from the outer margin of the anterior side; aperture subovate, prominent at the front; inner lip somewhat thickened at maturity; the outer lip extended at the front and its outer margin sinuous. The surface markings are irregular; sometimes more or less regular varices are perceptible. The proximal half of the spire is often marked with varices or more or less distinct wrinkles of growth. Length 17 mm., Diameter (last volution) 5.5 mm. (White 1887). Types in MNRJ.

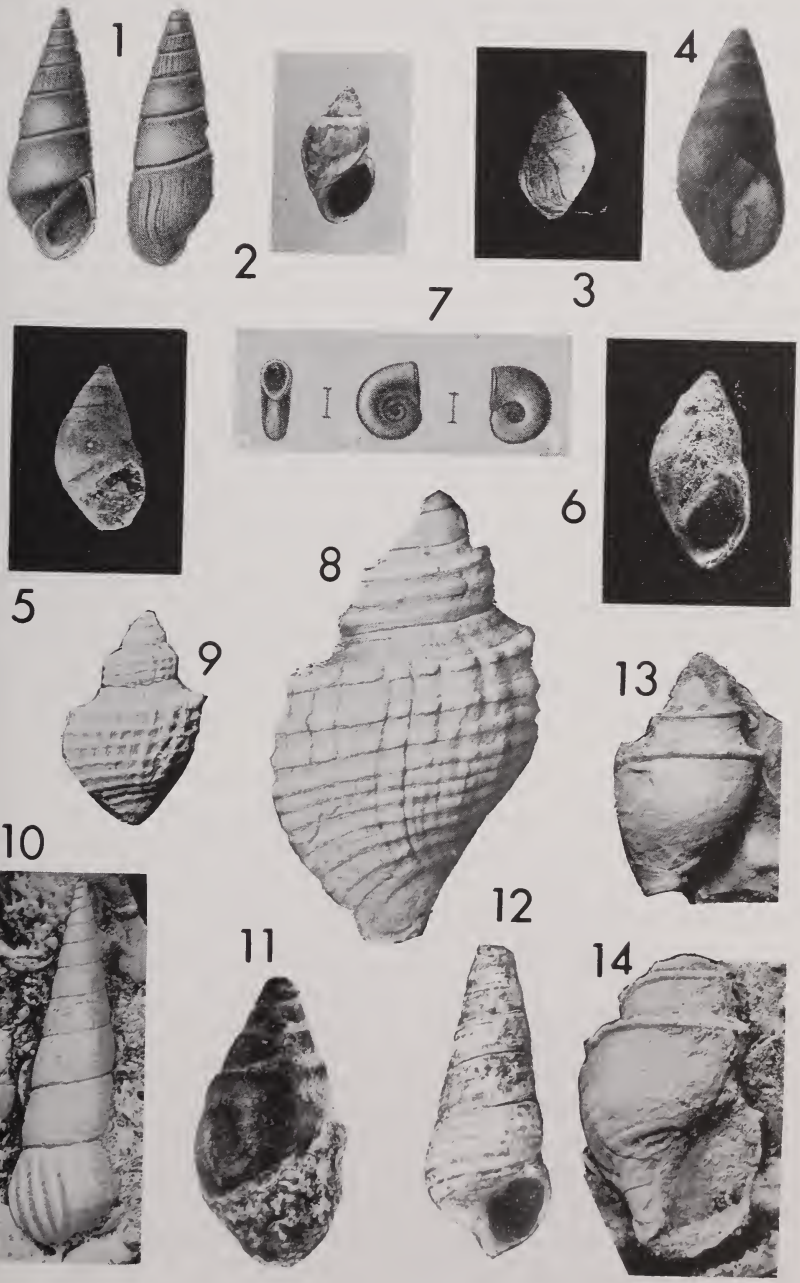
TYPE LOCALITY: From strata at Montserrate, Bahia, Brazil.

White remarked that associated with the type (adult) were many other specimens, juveniles, which could have been taken to be different species. To these probably belong the minute specimens (only 2.5 mm. long) named by Hartt *nicolayana*, also found with *terebriformis*. *Melania nicolayana* was never figured.

The Bahia series was formerly considered Cretaceous (Neocomian), but its

PLATE 15

1. *Pachychilus terebriformis* (Morris). x2.
2-6. *Paleoanculosa bullia* (Ihering). 4. Type, x1.
7. *Taphius monserratensis* (Hartt). x1.
8,9. *Pyrgulifera avus* (Pilsbry & Olsson). 8. Type, x5.
10. *Pachychilus gracillimus* (Pilsbry & Olsson). Type, x3.
11. *Paleoanculosa macrochilinoides* (Doello-Jurado). Type, x1 (from reproduction in Wichmann).
12. *Doryssa bibliana* (Marshall & Bowles). Type, x1.
13,14. *Aylacostoma (Verena) laevicarina* (Pilsbry & Olsson). 13. Type, x2.


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faunal contents, as well as its stratigraphical correlations, establish it as Paleocene. (see page 15.)

Pachychilus caboblanquensis Weisbord

Weisbord, 1962:482, pl. 1, figs. 1-3.

This species is known only by its holotype, of which only the last two whorls are well preserved. Indicated as a "Melaniidae" it is surely a *Pachychilus*, as identified by Dr. W. J. Clench.

ORIGINAL DESCRIPTION: "Shell of medium size, ovate, imperforate, substranslucent, rather thin but strong. Spire elevated, most of it missing. Sutures well defined, simple. Whorls slightly convex, number not known. Aperture large, oval, a little oblique. Outer lip broken but probably thin; basal lip effuse, not emarginate; lower lip thickened, somewhat reflected, the outer margin rather sharp. Columella and parietal wall calloused, the columella itself arcuate. Parietal wall obtusely angulated a little below the commissure; the angulation continues into the aperture but not on the wall proper. Ground color cream or buff with faint blotchy longitudinal bands of chestnut on the dorsum; the blotches show through the aperture. At the suture there is a narrow band of orange-brown bordered below by a narrow band with a pale, ashy tone. On the body whorl there is another ashen band, wider but vaguer than that near the suture, visible faintly on the dorsum below the periphery. Surface with exceedingly numerous granulose striae arrayed in spiral crinkles, as well as faint transverse growth markings, the former barely visible under a 10-power lens. L. 28 mm., D. 15 mm., L. of apert. 16 mm." (Weisbord).

TYPE LOCALITY: On hillside above west bank of Quebrada Mate Abajo, Cabo Blanco area, Venezuela. From Lower Mare formation, Middle Pliocene. Type in PRI.

This form belongs to the "species group" which Fischer & Crosse called *Cercimelania*, a synonym of *Pachychilus, sensu stricto*, according to Morrison. The color blotches remind one of *P. panucula* Morelet, but the specimen is closer in size to *P. indifferens* Fischer & Crosse (the latter two living species are from Guatemala).

?Pachychilus gracillimus (Pilsbry & Olsson)

Plate 15, fig. 10

Hemisinus (?) *gracillimus* Pilsbry & Olsson, 1935: 15, pl. 2, fig. 12.

The generic position of this species remains undecided. Evidently it does not belong to *Hemisinus*, but it seems to have affinities with *Pachychilus*. It is of extremely slender auger-like shape, with 10 flat-sided whorls, and two or three faint spiral lines below the suture. The diameter is less than one-third of its length: 16.5 mm. x 5 mm.

TYPE LOCALITY: West of Zopffs, La Cira formation, Magdalena Valley, Colombia. Upper Oligocene. Type in ANSP.

Subgenus *Glyptomelania* Fischer & Crosse, 1892
Type: *Melania glaphyrus* Morelet

Fischer & Crosse, 1892: 328.

This group has large shells with spiral, cord-like sculpture and large, variable nodules or tubercles. All species of this group offer great variability, and *M. glaphyrus* is exceedingly polymorphic. The living species are confined to Central America, but its fossils are known from far southern localities in Peru and Argentina.

Pachychilus (*Glyptomelania*) *bicarinata* (Fritzsche)

Melanoides bicarinata Fritzsche, 1924:19, pl. 1, fig. 10, text fig. 5.

This Fritzsche species is the only species of *Pachychilus* found in a region in which it has been replaced by *Doryssa*, differing entirely from *Melanoides* which is an Old World genus. As in the living species the Fritzsche form is very variable, and is similar to *P. glaphyrus*. Further materials and observations may prove that *Melanoides bicarinata* is an ancestral form of the living species. The fossil is not "*Melania bicarinata*" Etheridge, 1879, which subsequent authors placed in *Melanoides* (belonging to the so-called "Pebas" formation in Brazil containing Pleistocene, not Pliocene, fauna) but this secondary denomination does not invalidate the name *bicarinata* for Fritizsche's species. The Brazilian species described by Etheridge is probably *Dyris* (= *Conradia*).

Type in NR?

Pachychilus (*Glyptomelania*) *dimorphica* (Woods)

Melanatria dimorphica Woods, 1922:83, pl. 9, fig. 11.
Melanatria acanthica Woods, 1922:84, pl. 9, figs. 12-14.
Melanatria propinqua Woods, 1922:85, pl. 10, fig. 1.
Melanatria venusta Woods, 1922:85, pl. 10, fig. 2.

This species is related to the type of *Glyptomelania*, *P. glaphyrus*. The tubercles in *P. dimorphica* are less regular but stronger than in the tubercled *P. glaphyrus*, the sutures are well marked, and the aperture more angulated basally. In *M. venusta* a series of very variable spiral lines show below the sutural area, and more regular cord-like spirals on the upper whorl. The range of variations, from resemblance to *Doryssa* to well-tuberculed specimens, is as wide as in *P. glaphyrus*. Observing the variations of *Melanatria acanthica* and *M. propinqua*, Woods thought that "when more specimens are available they may

prove to be only varieties of *dimorphica.*" Considering the plasticity of the intergradated forms, all should be regarded as belonging to the same species.

TYPE LOCALITY: Negritos, NW. Peru, (the westernmost point on the Pacific coast of South America), from the "Turritella series," lower Negritos formation, upper Paleocene *(dimorphica+propinqua)*; also around La Brea, lower portion of *Clavalithes* series, upper Negritos formation, lower Eocene *(acanthica+venusta).* The species seems to have been very abundant at the time of Paleocene-Eocene transition.

Location of type: Sedgwick Museum, Cambridge, England.

Genus *Doryssa* H. & A. Adams, 1854
Type: *Melania atra* Bruguiere

H. & A. Adams, 1854:304.
= *Shepardiconcha* Marshall & Bowles, 1932.

Morrison (1954:367) mentioned the difficulty of separating the species of *Aylacostoma-Hemisinus-Shepardiconcha* from *Doryssa* by shell characters alone. *Doryssa* becomes more common southward than *Pachychilus,* although during the Tertiary both genera were widely and almost equally distributed. *Hemisinus* had many species from Colombia to Peru. *Shepardiconcha* (= *Doryssa*) is represented in the Eocene of California (Tejon formation), but is no longer living in North America. The fossil shells we include in this group are like those of *Turritella* (with spiral cords but lacking the strong tubercles of *Pachychilus*) although sometimes the fossils have very weak nodules.

Doryssa bibliana (Marshall & Bowles)
Plate 15, fig. 12
Plate 16, figs. 6, 8, 12

Shepardiconcha bibliana Marshall & Bowles, 1932:3, pl. 1, fig. 6.
Hemisinus (S.) biblianus, Palmer, 1941:400. pl. 6, figs. 1, 2.

The principal character in this species is the spiral sculpture consisting of five strong, cord-like, revolving lirae, with very weak nodules, plus an upper, stronger, one on each whorl marking a channel on the suture. The apex of the type is broken away, and the turritelliform shells had seven or eight gradually decreasing whorls. The type dimensions are: Length 20 mm., diameter 8.5 mm.

TYPE LOCALITY: Biblian, province of Canar, Ecuador, lower Miocene. Also from Paccha, prov. of Azuay in the Azogues sandstone (same strata with *Monocondylaea* and *Neocorbicula*). Azogues is upper Miocene. Palmer found this species to be

abundant in several localities near Azogues and Paccha, and in a series of several hundred specimens shows a great variability in sculpture, convexity of the whorls and suture. Type in USNM.

Doryssa andicola Pilsbry

Doryssa (?) *andicola* Pilsbry, 1939:69, pl. 1, figs. 1a, b. Ahlfeld, 1946: 174, pl. 7, fig. 2.

The shell is slender and has seven to eight very convex whorls with well-impressed suture; the three lower whorls with axial costulations, stronger at the middle, which in half of the body whorl are replaced by strong spiral cords (with sharp sulcations between), six to eight in number. Although present in upper whorls this sculpture is rather effaced. The aperture is not visible in the fossils known. The type with seven and one-half whorls (apex lost) measures: L. 13.5 mm., D. 4 mm.; another specimen, almost complete, is 18 mm. long.

TYPE LOCALITY: El Molino, near Potosí, Bolivia, upper Puca strata, Paleocene.

As Pilsbry indicated, the generic position of *D. andicola* is still open to question, but in a wide sense it agrees better with *Doryssa* than with any other group. It resembles *Pachychilus drakei* Arnold & Hannibal (Hannibal 1912:183, pl. 8, fig. 26), from the Tejon formation, Eocene, of Little Falls, Washington, but it is closer to *D. maimarensis* (Bonarelli) from the Paleocene of northwestern Argentina. It also can be compared with the living *D. transversa* (Lea) from Guayanas and Brazil (see Note 50).

Doryssa (sensu lato) maimarensis (Bonarelli)

Zygopleura maimarensis Bonarelli, 1921:70, pl. 9, fig. 8. 1927:91, pl. 4, fig. 7.

Zygopleura crassinodis Bonarelli, 1927:88, pl. 4, fig. 1 (and 2?)
Zygopleura scopesi Bonarelli, 1927:89, pl. 4, fig. 3.
Zygopleura paucinodosa Cossmann (in part), 1925:200.
Zygopleura multicosta Bonarelli, 1921:70, pl. 9, fig. 12 (not 13). 1927: 89, pl. 4, fig. 4.
Zygopleura gallardoi Bonarelli, 1921.70, pl. 9, figs. 14, 15. 1927:90, pl. 4, fig. 5.
Zygopleura pustulosa Bonarelli, 1921:70, pl. 9, fig. 17. 1927: 90 pl. 4, fig. 6.
Katosira longobardii Bonarelli, 1927:92, pl. 4, fig. 8.
Katosira percrassa Bonarelli, 1927:93, pl. 4, fig. 9.
Katosira groeberi Bonarelli, 1927:93, pl. 4, fig. 10.
Katosira nagerai Bonarelli, 1927:94, pl. 4, fig. 11.

All the specimens figured by Bonarelli in 1927, plate 4, under *Zygopleura* and *Katosira* represent variations of the same species, which has a long and many-spiraled shell (at least 9 whorls can be counted in *K. longobardii*). The sutures are well marked and the nodules vary from six to eight. The spiral cords are better marked in those named *K. groeberi* and *K. percrassa*. As in *D. andicola*, all these named "species" or "forms" can be placed in *Doryssa, sensu lato* (the strata in which *D. andicola* was found in Bolivia are the same as those of *D. maimarensis*).

Doryssa maimarensis, with all its variations, can be distinguished from the fossils of other localities described by Bonarelli, which belong to *Pachychilus* and *Potamides*.

TYPE LOCALITY: Maimará Station (railroad to La Quiaca) on the left margin of the Humahuaca River (Quebrada de Humahuaca), prov. of Jujuy, N.W. Argentina, in Paleocene strata of the upper (fresh-water) Puca formation (Mirafloran), which Bonarelli had considered marine and Triassic (see Notes 2 and 3).

Doryssa corrosensis (Pilsbry & Olsson)

Hemisinus (Basistoma) corrosensis Pilsbry & Olsson, 1935:12, pl. 2, figs. 8, 9.

The authors compared this species with *Hemisinus brasiliensis* Moricand, which probably is an *Aylacostoma (Hemisinus)*, but *D. corrosensis* is very different. It does not belong to *Basistoma*, and the shell characters: many cord-like spirals, fine-suture, small aperture, and flatness of whorls, indicate a *Doryssa* of the group of the type species *D. atra*.

The dimensions of the type specimen are: Length 29 mm., diameter 11 mm. (five whorls). When complete it must have had not less than seven whorls. Another specimen (Pilsbry & Olsson, fig. 9) is shorter, with only four whorls remaining, reaches the latitude of the upper suture of the second whorl in the type, and is stouter. Thus the species is very variable in proportions.

TYPE LOCALITY: Sucio River, a branch of Llano River. S.E. of Infantas and W. of the Magdalena River, Colombia. Los Corros formation, upper Eocene. Type in ANSP.

Family THIARIDAE

Since the principal differences between the Thiaridae and Pleuroceridae are found in their reproductive systems — most, although not

all, Thiaridae being parthenogenetic — and the shell characters offer many cases of convergence, the classification of fossils in these groups is very difficult. The Tertiary fauna is here arranged according to the general systems of Pilsbry, Morrison, and Wenz:

Genus *Pyrgulifera*
Genus *Aylacostoma*
 Subgenus *Hemisinus*
 Subgenus *Verena*
 Subgenus *Longiverena*
Genus *Hannatoma*
Genus *Morgania*

Genus *Pyrgulifera* Meek, 1877

Type: *P. humerosa* Meek
Cretaceous, Wyoming

= *Hantkenia* Fischer, 1885.

The name *Pyrgulifera* was introduced first by Meek in 1872, for his *Melania humerosa* of the Bear River formation in Wyoming, but it was not fully described until 1877. White (1895) produced a revision of the genus, indicating it as the most characteristic of the Bear River Cretaceous fauna, also known from non-marine strata, approximately of the same age, in Europe. *Paramelania* E. A. Smith, 1881, an African living group of Lake Tanganyika, was considered a synonym, but Pilsbry & Bequaert (1927) made a definite separation between them. While *Pyrgulifera* by its affinities to the neotropical genus *Aylacostoma,* is a Thiaridae, Morrison (1954) placed *Paramelania* in Pleuroceridae. More recently, Yen (1958) concluded that the resemblance between *Paramelania* and *Pyrgulifera* is only superficial.

Pyrgulifera is closest in relationship to the subgenus *Verena* of the *Aylacostoma.* Pilsbry and Olsson (1935) described several species as *Verena* and *Longiverena* from the Magdalena Valley in Colombia. Although separated from them in time and space, *Pyrgulifera* appears to be intermediate in characteristics between these latter two groups, and is probably their ancestor, with a distribution in North and South America from mid-upper Cretaceous to Paleocene, and extinct today.

Yen recognized 21 species and subspecies, eight from the Cenomanian of Wyoming and Texas, and 13 from the Senonian of Europe, in

France and Hungary. Lately, in another revision, Rey (1961), extended the range to Australasia, with *P. glypta* Rey & Arias from the Senonian of New Caledonia. Rey also made a revision into subgenus *Hantkenia*, with rounded, subglobular whorls, and *Tanaliopsis* for trochoid forms. But the three South American species whose descriptions are given here are *Pyrgulifera, sensu stricto.*

Most of these Paleocene species were found in strata containing "*Corbicula*" and "*Unio*" in Europe and North America. On some occasions a brackish-water habitat was revealed, or marine-estuarine species were also present, as occurs in the South American forms. But neither Yen nor Rey had opportunity to record the genus for South America.

In 1927, Bonarelli described a new genus and species, *Brachycerithium feruglioi* from the dolomitic limestones of Tres Cruces, a locality near the Bolivian border in the province of Jujuy, Argentina. [The relative age of the strata (also containing many *Doryssa*) was supposed to be between the upper Triassic (Keuper) and lower Jurassic (Lias), and the strata to be marine sediments.] *Brachycerithium feruglioi* belongs to the same group of the type of *Pyrgulifera, P. humerosa.* Furthermore, the species *B. feruglioi* is so entirely distinct from the type of *Brachycerithium (B. majus* Bonarelli) that they cannot be congeneric, as Grœber observed (in Bonarelli, 1927).

Pyrgulifera feruglioi (Bonarelli)

Plate 16, figs. 7, 9.

Brachycerithium feruglioi Bonarelli, 1927:112, pl. 6, figs. 10-13.

ORIGINAL DESCRIPTION: (translation): Shell conic-turreted, spire gradated, spiral angle 40-45°, whorls angulated, with costulae which are nodulous on the shoulder; columella strong and straight; with spiral striae, but smooth on the posterior side; peristome oval."

The author did not indicate dimensions, but according to the illustrations, the type is approximately 19.5 mm. in length and 11 mm. in diameter. Another figured specimen is only 12.5 mm. x 6.5 mm. This last one clearly shows the spiral cords at the base.

TYPE LOCALITY: (given in the subtitle of the third part of the paper, page 98): Tres Cruces, in "horizonte calcareo-dolomitico," 70 miles S. of La Quiaca, Province of Jujuy, Argentina.

Otto Haas (1953), studying late Triassic gastropods from central Peru, included *Brachycerithium* as a subgenus of *Paracerithium* (marine) and so considered the Tres Cruces fauna approximately contemporary with that of Noarian and Rhetic in Peru. While a discussion of

the Triassic marine fauna from Peru is not pertinent here, it should be made clear that *Pyrgulifera feruglioi* has no relation with those Mesozoic fossils.

The controversy about the relative age of the dolomitic limestones of Tres Cruces — Maimará area — lasted for decades. Schlaginweit (1941), Frenguelli (1937), and Ahlfeld (1946), estimated that the strata cannot be older than the uppermost Cretaceous, and Grœber (1939b) came closest to the correct age: Danian. All these authors concur on the fresh-brackish-water condition of the fauna, and also synchronized its fossils with those of the Puca formation of Peru and Bolivia, from which Fritzsche and Pilsbry had described other species. From coeval sediments at Yaví in the same province of Jujuy, close to the type locality of *P. feruglioi*, Fritzsche described Corbiculidae and Valvatidae. And the geologist G. Steinmann also collected abundant materials of fresh-water fauna and contemporary flora from Tres Cruces.

Pyrgulifera sehuena, new species

Plate 13, figs. 1-4

DESCRIPTION: Shell very solid, of medium size. Spire turreted, elevated, ending acutely. Nuclear whorls showing (in some inner casts) obsolete axial riblets, sunk obliquely and surrounded by the next volution. Post-nuclear whorls more conspicuously ribbed (about 10 axial ribs). Five shouldered whorls (less gradate than in other species of the genus, with obscure carina and submarginated suture. The axial costulae or ribs continuing to the last whorl, where they become diffuse at the base. Spiral cords progressively stronger from the third whorl to the base, 8-10 in number in the last whorl. At the crossing of the axial and spiral sculpture there is a tendency to form nodules or imbrications. Interspaces concave. Aperture oval, slightly angulate at both ends, with columellar wall wide and thicker than at the base, without a canal.

DIMENSIONS: Type: length 26.5, diameter 15 mm., lesser diameter 14 mm., last whorl 19.5 mm., sutural inclination 12°. Larger paratype: length 26.5, diameter 17 mm. Other paratypes are proportionally wider, but the exact length is not measurable because of their fractured apexes or bases.

TYPE LOCALITY: West margin of Lake Amenida, 8 miles S. of Sehuen River (also called Chalia), and S.E. of Mata Amarilla, province of Santa Cruz, Argentina. From Sehuenan beds, Danian. 19 paratypes; collected by E. Feruglio, 1935. Type in CM., paratypes in MACN.

The paratypes are very variable. Some show stronger crossed sculpture than other species of *Pyrgulifera*, and occasionally the suture is marginated or beaded. The thick columellar wall in *P. sehuena* has

similarities to that of *P. stantoni* from Wyoming. Elongated specimens with well-marked axial ribs resemble *P. humerosa cokevillensis*. Others are shorter and rather globose, less carinated than European species of the same size and shape, but always with stronger sculpture. By all these characters *P. sehuena* has closer relationships to *P. stantoni*, but is a more compact form.

Pyrgulifera sehuena resembles *P. avus* (Pilsbry) from the Oligocene of Colombia, and both are younger than any North American or European species, showing an evolutive line toward a more complete network of axial and spiral ribs. In *Verena* a further modification took place with the disappearance of the axial ribs, and the remaining spiral cords are stronger.

The southernmost strata, where *P. sehuena* was found, were the subject of an extensive paper published by Feruglio in 1938, indicating a Senonian age, and a possibility that the upper part is Danian. These deposits reappear in the north at Chubut in Colhue Huapi, with *Potamides* and *Diplodon*. Deposition took place when the San Jorge Sea was in regression. (See page 21 and Notes 8, 9, 10.)

?Pyrgulifera avus (Pilsbry)

Plate 15, figs. 8, 9

Hemisinus (Verena) avus Pilsbry & Olsson, 1935:15, pl. 3, figs. 6, 7 [Not *Hemisinus avus* Pilsbry, 1944 = *palaeus* Pilsbry, 1964, new name.]

The assignment of *H. avus* to *Pyrgulifera* is only provisory, but it certainly differs from any other known *Hemisinus*, and may be an intermediate between *Verena* and *Pyrgulifera*. It has a short, gradate spire, and sculpture combining nodulous, axial, and spiral ribs, resulting in a reticulated pattern except at the base. The outline, as in most species of *Pyrgulifera*, is very variable: some specimens have obsolete ribs, others 12 spiral cords in the last whorl. Pilsbry compared it with *H. crenocarina* (Moricand), which is the type of *Verena* with spiral sculpture only. The largest specimen measures 12 mm. in length and 7 mm. in diameter.

TYPE LOCALITY: La Cira district near Zopffs, Magdalena Valley, Colombia, from La Cira formation, Oligocene (see page 28). Type in ANSP.

Subfamily AYLACOSTOMINAE (Hemisinu-eae Wenz)

Genus *Aylacostoma* Spix, 1827

Type: Subsequent designation Morrison, 1952,
Aylacostoma glabrum Spix
= *Melania scalare* Wagner

This group includes turritelliform shells with whorls almost flat, spiral sulcation, elongated aperture, and angulation at both ends, with expanded lip. Living forms usually have color dots or markings arranged spirally. *Aylacostoma, sensu stricto,* ranges from Central America to Brazil and some living species are known from the Argentine province of Corrientes (*A. chlorotica* and *A. stigmatica* H. Scott) on the big bend of the Paraná River.

Aylacostoma sigmachilus (Pilsbry & Olsson)

Hemisinus sigmachilus Pilsbry & Olsson, 1935:11, pl. 2, figs. 10, 11.

ORIGINAL DESCRIPTION: "Shell oblong-conic, diameter less than half of the length, whorls slightly convex, smooth except for weak lines of growth which have a reversed S trend, being retracted in a rather deep bay between suture and periphery, then arching broadly forward, much as in *H. edwardsi* (Lea). There is a more or less marked contraction or concavity immediately below the suture, which in crushed specimens may appear as a distinct margination of the suture. The aperture is ovate, the columella moderately thick." Length 20.5 mm., diameter 11 mm.; 3½ whorls preserved.

TYPE LOCALITY: Rio Llano, Magdalena Valley, Colombia, from Mugrosa formation, Oligocene. Type in ANSP.

Compared with living species it approaches *Aylacostoma obesa* (Reeve) from Brazil; shape, proportions, and sigmoid lines are almost identical.

Aylacostoma sulcatus (Conrad)

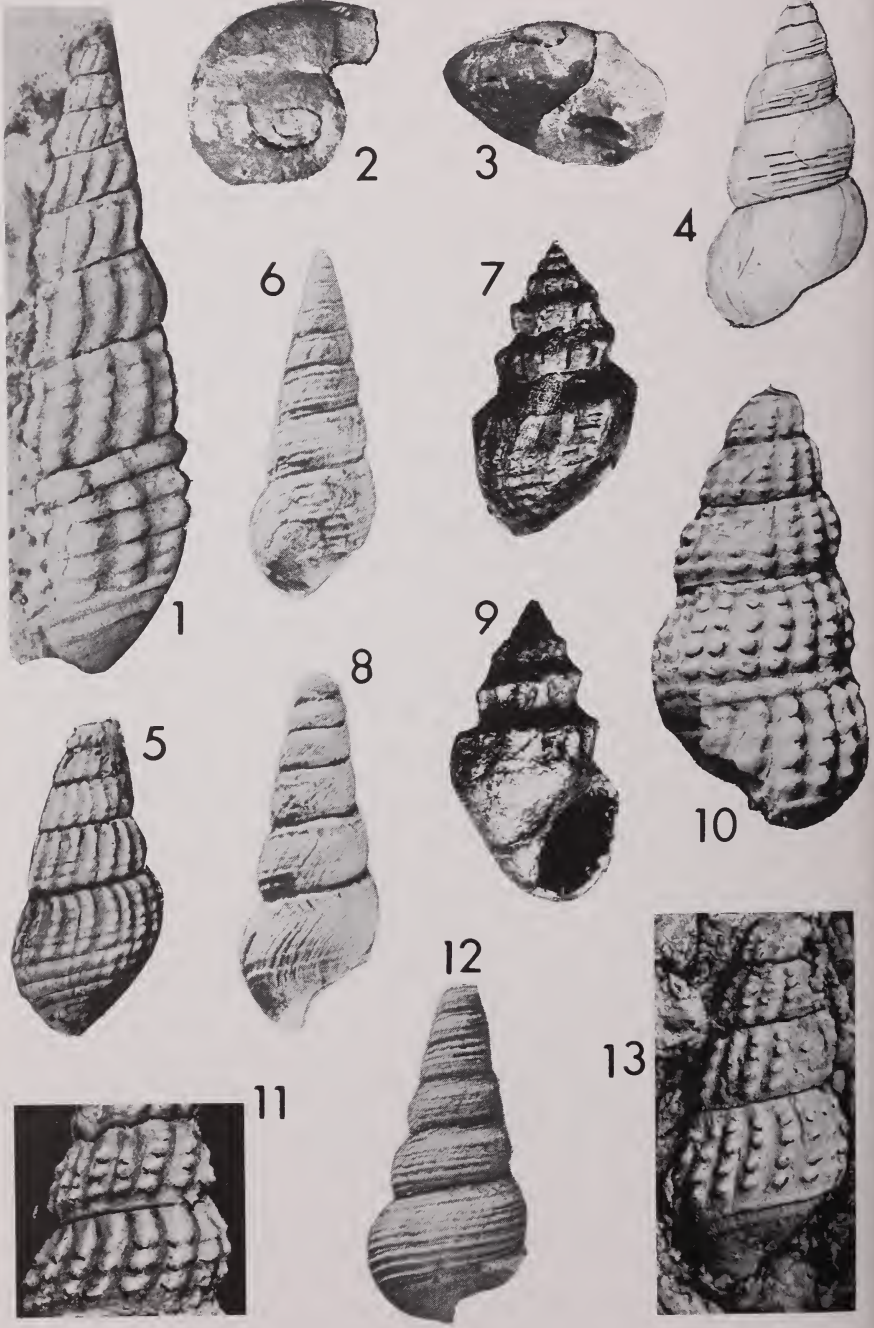
Plate 14, figs. 6, 7

Hemisinus sulcatus Conrad, 1871:194, pl. 10, fig. 12.
Melanopsis (?) *browni* Etheridge, 1879.

Semisinus sulcatus, de Greve, 1938:99, pl. 4, figs. 17-19, 21-25.

This species is easily identifiable by its relatively constant characteristics: fusiform-scalated, with many revolving ribs stronger at the shoulder, and lip broadly expanded and sinuous.

I have observed numerous specimens (Plate 14) obtained from Servico Geologico do Brasil, collected at the Javary River near Tres Unidos, which have been labeled *Melanopsis browni* Etheridge. *A. sulcatus*


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seems to be of the group of living species *A. rubiginosus* and *A. tenellus* (Reeve) from Brazil, but is decidedly different.

TYPE LOCALITY: Pebas formation, upper Pliocene, Peru. Those mentioned from Brazil are more likely Pleistocene. Type in ANSP.

Subgenus *Hemisinus* Swainson, 1840

Type: *Melania lineolata* Gray

= *Semisinus* Fischer, 1885.

This subgenus is characterized by its form, broader and shorter than in *Aylacostoma, sensu stricto,* and the absence of spiral sculpture. Many of the fossil species named under *Hemisinus* belong to other subgenera. The distribution extends from Central America and the West Indies to western South America in Ecuador and Peru.

Aylacostoma (Hemisinus) tuberculifera (Conrad)

Hemisinus tuberculiferus Conrad, 1874b:83, pl. 12, fig. 4.
Sheppardiconcha (?) *tuberculiferus,* Marshall & Bowles, 1932:4.
Semisinus tuberculiferus, de Greve, 1938:101, pl. 3, figs. 31-33; pl. 4, figs. 1, 6, 12.
Semisinus peyeri de Greve (in part), 1938:104, pl. 4, figs. 7-11.
Hemisinus (Sheppardiconcha) tuberculiferus, Pilsbry, 1944:152, pl. 11, fig. 26.

The name *A. tuberculiferus* [*fera*] should not be confused with that of *Aylacostoma tuberculatus* Spix, which is the type of subgenus *Longiverena.*

ORIGINAL DESCRIPTION: "Turreted, elongated, volutions 9, laterally straight; three prominent revolving tuberculated ribs on each volution of the spire, except two or three nearest the apex; last volution with 9-10 revolving lines unequal in size; a fine carinated line borders the upper margin of the suture, which is indistinctly defined; aperture short."

TYPE LOCALITY: Pebas, Iquitos region, Peru, from Pebas formation, upper Pliocene. Type in ANSP.

PLATE 16

1. *Aylacostoma (Longiverena) waringi* (Pilsbry & Olsson). Type, x6.
2,3. *Poteria (Pseudopaerostoma) bibliana* (Marshall). Type, x1.
4. *Lyrodes laciranus* (Pilsbry & Olsson). Type, x10.
5. *Aylacostoma (Longiverena) mugrosana* (Pilsbry & Olsson). Type, x2.
6,8,12. *Doryssa bibliana* (Marshall & Bowles). x1.
7,9. *Pyrgulifera feruglioi* (Bonarelli). Type, x1.
10,11,13. *Aylacostoma (Longiverena) eucosmius* (Pilsbry & Olsson). 13. Type, x2½.

On Pilsbry's specimens (1944, fig. 26), as well as many of those figured by de Greve, the nodules or tuberculae of the spiral ribs are worn off, but all are of the same species, strata, and locality. On this account de Greve thought that the best preserved specimens with tuberculae were a distinct species which he called *Semisinus peyeri*. In a long series of specimens, both forms are inseparable. *Doryssa bibliana* (Marshall & Bowles) resembles those worn specimens of *A. tuberculifera*, but it is a Thiaridae from the lower Miocene strata of Ecuador.

Conrad (1874a:32, pl. 1, fig. 14) also described, from the same Pebas formation, *Hemisinus sterei*. This has a more scalariform shell, without tuberculae, and the revolving carina appears only at the body whorl and suture. The only (poorly preserved) specimen, may be *A. tuberculifera* or an intermediate with *A. sulcatus* Conrad. In fact some of the figured *A. tuberculifera* in de Greve also approach *A. sulcatus*.

Aylacostoma (Hemisinus) pictus (Pilsbry)

Hemisinus pictus Pilsbry, 1944:146, pl. 11, fig. 30.

The type, and only specimen known, is a fragment of shell of only two whorls, 10 mm. long, without sculpture but with a preserved pigment showing a series of axial, short, dark-brown dashes, or dots, similar to those of some living species. According to Pilsbry it may belong to the group of *A. (H.) lineolatus* (Wood).

TYPE LOCALITY: Upstream from San Antonio, Pachitea River, province Huanaco, central Peru, in fine-grained limestone shale. Oligocene. Type in ANSP.

Subgenus *Verena* H. & A. Adams, 1854

Type: *Melania crenocarina* Moricand

= *Gonioconcha* Bonarelli 1921

(Note 51)

Verena includes the shorter, stout forms of *Aylacostoma*, with larger body whorl, spire gradate-pyramidal, strong spiral ribs, tuberculate-carinate shoulder, broadly expanded aperture with a short canal at the upper right end, columellar lip very sinuous, and outer lip festoon-like. It is the living South American group closest to the fossil *Pyrgulifera*, but it lacks the axial costulae.

The Recent species is distributed only in northern South America.

Aylacostoma (Verena) striata (Bonarelli)

Gonioconcha striata Bonarelli, 1921:72, pl. 9, figs. 33-34. 1927:101, pl. 5, fig. 3.

Gonioconcha striato-spinata Bonarelli, 1921:72, Pl. 9, figs. 35-37. 1927: 101, pl. 5, fig. 4.

Gonioconcha spinata Bonarelli, 1921:72, pl. 10, fig. 29. 1927:102, pl. 5, fig. 5.

Gonioconcha nodosa Bonarelli, 1921:72, pl. 10, fig. 5. 1927:102, pl. 5, fig. 7.

DESCRIPTION: Shell small, turriform, short spire, carinate with four to six low carinae, and sometimes non-carinate, gradate but with whorls sometimes convex, suture well-impressed, basal lip produced.

TYPE LOCALITY: Tres Cruces, province of Jujuy, Argentina; from the "Calcareo-dolomítico." Paleocene.

Besides the listed synonyms in the 1927 paper, Bonarelli named some "varieties" *(brachyspira, evolutior)* which are unidentifiable.

Aylacostoma (Verena) brackebuschi (Bonarelli)

Hypsipleura (?) *brackebuschi* Bonarelli, 1927:76, pl. 2, fig. 16.

Bonarelli established *H. brackebuschi* as a "form" (all Bonarelli's descriptions are of forms or varieties, never species) based on a fragment consisting of the last two whorls, which are gradate with conspicuous cord-like carinae on the shoulder below suture. The author did not give dimensions but judging from the type figure it must have been a large, many-spiraled species, with some resemblance to *A. (V.) laevicarina*, but the last whorl is decidedly shorter.

TYPE LOCALITY: Carbajal, S.W. of Rosario de Lerma, a short distance from the Lerma "pucará." In the "Calcareo-dolomítico," Paleocene.

Hypsipleura, a Loxonematidae from the Triassic-Jurassic of Europe is entirely different.

Aylacostoma (Verena) laevicarina (Pilsbry & Olsson)

Plate 15, figs. 13, 14

Hemisinus (Verena) laevicarina Pilsbry & Olsson, 1935:15, pl. 13, figs. 10-12.

This species agrees well with the characteristics of *Verena* and differs from the type species *A. crenocarina* from Brazil in being higher, but it has the same evenly sharp carina marking the shoulder, above which the whorl is concave, and gradate (as in *A. brackebuschi*). The last whorl has about ten cord-like spirals, not strongly marked but visible on the columellar side. The basal sinus is distinct. The dimensions are: length 17.5 mm., diameter 11 mm.

TYPE LOCALITY: Oponcito River, near Guanabanas. E. of the Magdalena River, Colombia, from La Cira formation, upper Oligocene. Type in ANSP.

Subgenus *Longiverena* Pilsbry & Olsson, 1935

Type (subsequent designation Morrison, 1952):
Aylacostoma tuberculatum Spix
= *Melania tuberculata* Wagner, not Müller

This group was created as a "section" of *Hemisinus*. It combines the gradate form of *Verena* with elongate shells as in *Aylacostoma, sensu stricto,* plus a sculpture of crossed costulae and spiral sulcations, resulting in a granulated surface. The aperture is like that in *Verena* but less expanded. By convergence, some species resemble *Doryssa* in the Pleuroceridae. With the exception of *S. peyeri,* which is an uncertain form, all other fossil species are from the Oligocene of Colombia and Peru.

Aylacostoma (Longiverena) eucosmius (Pilsbry & Olsson)
Plate 16, figs. 10, 11, 13

Hemisinus (Longiverena) eucosmius Pilsbry & Olsson, 1935:13, pl. 3, fig. 2.
Hemisinus (Longiverena) lapazanus Pilsbry & Olsson, 1935:13, pl. 3, fig. 3-4.
Hemisinus (Longiverena) hopkinsi Pilsbry & Olsson, 1935:14, pl. 3, fig. 8.
Hemisinus (Longiverena) laciranus Pilsbry & Olsson, 1935:14, Pl. 3, fig. 5.

The four names indicated above should be considered samples of one and the same variable species, as individuals of different stages of growth, probably clones, but not specifically distinct. The differences among them show variation in the convexity of the whorls, and in the number of tubercles in each whorl. Observing the extraordinary polymorphism that exists in other living species of this group, as in *A. rubuginosus* Morelet from Guatemala, it is not unlikely that fossil species are just as variable. Fischer and Crosse thought that such variations (common in all the "melanias," Thiaridae as well as Pleuroceridae), represent sexual dimorphism. But since the Thiaridae are mostly parthenogenetic (Morrison, 1954 states that "there are no male individuals known in the entire family"), direct-lineage populations may account for such polymorphism. In fossil shells, of course, this fact can-

not be physiologically proved, and the assumption is probably based on very similar reproductive conditions of ancestors and descendants. Quoting Morrison again, "*what we have in the entire family of the Thiaridae is the possibility of clone formation in every existing population.*" (Emphasis mine.)

COMBINED DESCRIPTION: Shell conic-turreted, sometimes slender (*H. eucosmius*) or broader at the base (*H. hopkinsi*). The apex is unknown in all the "species," but the estimated number of whorls for all is between 5 and 6. The whorls may be decidely convex (*H. lapazanus*) or somewhat flattened on the left side (dorsal view of *H. eucosmius*). Suture rather deep, which in the larger, gerontic, specimens develops a margination. The sculpture consists of axial ribs broken into tubercles arranged in spiral rows; the number of these tubercles, from suture to suture, is normally 3, sometimes 3-4 (*H. eucosmius*) or 5 (*H. hopkinsi*). In some individuals the spiral lines dividing the tubercles are more conspicuously continuous (*H. lapazanus*). The tubercled axial ribs terminate below the middle of last whorl and below are replaced by spiral cords, the upper one being stronger. Below the cords the base shows only lines of growth. The aperture in all specimens is concealed in the matrix, or broken.

DIMENSIONS: of the type (*H. eucosmius*): Length 12.3 mm., diameter 5.6 mm., based on the only three preserved whorls. Other specimens measure: L. 14 mm., D. 7 mm. (4½ whorls, *H. lapazanus*); L. 15 mm., D. 7.5 mm. (5 whorls, *H. hopkinsi*); and the smallest, L. 15 mm., D. 7 mm. (3 whorls, *H. laciranus*). Thus, the average size of specimens with 3 whorls is: L. 13.7 mm., D. 6.3 mm. Type in ANSP.

TYPE LOCALITY: Mugrosa, 30 miles E. of Magdalena River, and S. of Barranca Bermeja, Colombia, in the Mugrosa formation, lower-middle Oligocene. Others are from El Centro *(H. lapazanus, H. hopkinsi)* in the same formation, and near La Cira (*H. laciranus*), from La Cira formation, Upper Oligocene. All the specimens were collected by O. C. Wheeler.

Aylacostoma (Longiverena) paleus (Pilsbry)

Hemisinus paleus Pilsbry, 1950:69, (new name for *Hemisinus avus* Pilsbry, 1944, not *H. avus* Pilsbry, 1935 = *Pyrgulifera*).

Imperfectly known, from fragments, *A.* (*L.*) *paleus* shows oblique axial ribs, 5 in the last three preserved whorls. Spaces between ribs filled with spiral-cord-like lines (6 in the last whorl). Whorls normally convex, and suture impressed. L. 20 mm., D. 7 mm. Compared with *S. peyeri* de Greve, in which Pilsbry found similarities, it differs by having no tubercles.

TYPE LOCALITY: Upstream from Quebrada Sungarillo, Pachitea River, Peru. Oligocene. Collected by J. T. Singewald in 1926. Type in ANSP.

Aylacostoma (Longiverena) mugrosana (Pilsbry & Olsson)
Plate 16, fig. 5

Hemisinus (Longiverena) mugrosanus Pilsbry & Olsson, 1935:13, pl. 3, fig. 1.

ORIGINAL DESCRIPTION: "The conic shell is straight-sided, the diameter contained about 2.4 times in the length. The whorls are flat but joined by a deeply impressed suture. Sculpture of axial ribs which are rounded and about equal to their intervals, somewhat curved, being retracted a little below the suture, then advancing and gradually disappearing at the periphery of last whorl; on the last half turn there are about eleven ribs. Spiral sculpture of grooves cutting the ribs more deeply than the intervals, 5 on the penultimate whorl of the type, the lowest grooves wider. The lines of growth have a reversed sigmoid trend, advancing in a broad curve on the base, retracted somewhat near the suture. The aperture has the narrow basal spout of *Hemisinus*. Columella moderately thick. L. 18.6 mm., D. 9 mm; 4½ whorls remaining."

TYPE LOCALITY: Llano River, Magdalena Valley, Colombia, in the Mugrosa formation, Oligocene. Type in ANSP.

This species is very close to *A. eucosmius*, with about the same average size, but the whorls are flatter, with deep sutures, and the tubercles more numerous and compact in axial line, forming almost continuous costulae. The spiral cords at the base are also more conspicuous. The closest affinity is with the form *lapazanus* (of *A. eucosmius*).

Aylacostoma (Longiverena) waringi (Pilsbry & Olsson)
Plate 16, fig. 1

Hemisinus (Longiverena) waringi Pilsbry & Olsson, 1935:14, pl. 3, fig. 9.

This is the longest and slenderest, in proportion to its diameter, of all the *Aylacostoma* from the Oligocene of Colombia. It also has the largest number of whorls (nine preserved in the cast type), which are slightly convex. The sculpture, as in *A. mugrosana*, is composed of nodulous ribs, but the spiral lines are more deeply marked, especially in the last three whorls. In the upper whorls the tubercles are less distinct, and the ribs appear to be complete. On account of the shell length, the suture is more oblique. The length is 14 mm. and the diameter 5 mm.

TYPE LOCALITY: Near Zopffs, La Cira district of the Magdalena Valley, Colombia, from La Cira formation, upper Oligocene, Type in ANSP.

Aylacostoma (Longiverena) peyeri (de Greve)

Semisinus peyeri de Greve, 1938:104, pl. 4, figs. 7-11.

As indicated previously (page 144), the characters of this species approach those of *A. tuberculifera*, but as there also seems to be a relationship to the *A. eucosmius* group, *A. peyeri* probably represents a transition between *Verena* and *Longiverena*. The species is about the same size as *A. eucosmius* (L. 11.3 - 12.4 mm., D. 4.7 - 5.4 mm.; aper-

ture 3.7 - 4.6 mm.). The contour is slender and the tubercles (about eight in the dorsal view of the last whorl) are very regular, with five spiral cords at the base. The aperture is rounded, and canaliculate at the base. The whorls are relatively convex.

TYPE LOCALITY: Iquitos region, Peru, from Pebas formation, Pliocene. Type in ZIUZ.

Aylacostoma (Longiverena) peyeri dickersoni (Palmer)

Hemisinus (L.) peyeri dickersoni Palmer, 1941:398, pl. 6, figs. 15-18.

Differs from *A. peyeri peyeri* by its blunter ribs and narrower interspaces; the ribs are also less nodulous (observation based on worn specimens). It has similarities to *A. eucosmius.*

Palmer did not describe this form as a subspecies but as a "variety." Pilsbry (1944:146) thought that *A. dickersoni* is specifically distinct from *A. peyeri.* But in describing other fragments of shells as *Hemisinus avus* (1944:145), which he subsequently renamed *A. paleus*, he doubted that this latter form was really different from *A. dickersoni,* as the only variation (in the sculpture) was slight. On the other hand, *A. paleus* is from the Oligocene of Peru, and *A. peyeri dickersoni* is from west of Cojitambo at Arroyo Potrero, in the vicinity of Cuenca, Ecuador, and was found in middle Miocene strata. The type is in PRI.

Genus *Hannatoma* Olsson, 1931

Type: *Melanatria gesteri* Hanna & Israelsky

Hannatoma gesteri (Hanna & Israelsky)

Hanna & Israelsky, 1925:42, pl. 8. Wenz, 1961:717, fig. 2073.

I have not seen this species. According to the description it has shouldered whorls, sulcated at the middle, and the base has four strong cord-like carinae. It is of large size: L. 50 mm., D. 24 mm.

TYPE LOCALITY: Punta Sal Chico, Peru, in Negritos formation, Oligocene.

Another genus described by Olsson in 1931 was *Anconia* (type *A. elenensis* Olsson, from Punta Ancon, Ecuador, Oligocene). The genus was placed within the "Hemisinueae" by Wenz (1961:717, fig. 2074), but its systematic position is uncertain. It is a shell of extraordinary size, and even with a broken apex is 93 mm. long. When complete it must have measured more than 100 mm. It has seven (and perhaps had

10) whorls, is very slender from the penultimate whorl up, convex, and has a well marked suture. The last whorl is sculptured with oblique and undulating axial ribs. It approaches *Basistoma* but is without the spirals.

Genus *Morgania* Cossmann, 1906

Type: *Vicarya fusiformis* Hislop

The family group of this genus has not been satisfactorily decided. The Eocene species from Peru are probably Thiaridae (Melanopsinae), but Wenz includes the type in *Morgania* as a subgenus of *Vicarya* from the Eocene of India (1961:742, fig. 2146), in the Potamididae. Perhaps the South American fossils should be separated under a new generic or subgeneric name. Until other materials are found and relationships better known, the species are listed here, only provisorily, under *?Morgania.*

The shells are lanceolate, tapering to a very slender apex, without sculpture except for lines of growth and very close spiral cords at the base. The aperture is very peculiar, with thick, arched columella and a siphonal base on the outer lip obliquely curved, the upper part of it curved in the opposite direction, forming a sinus. The sutures are sharply oblique and the spire is somewhat contorted on the upper half, as in some Melanellidae.

?Morgania magna Woods

Woods, *in* Bosworth, 1922:82, pl. 9, figs. 5, 6.

ORIGINAL DESCRIPTION: "Shell elongate, broadest in front of the middle. Spire long, of about nine whorls, which are flattened; sutures linear. A few of the early whorls with fine spirals and stronger transverse ornament, other whorls smooth except for growth lines. Part of the penultimate and last whorl often more convex than the preceding whorls. On the anterior part of the last whorl are four strong spiral ribs at the level of the posterior half of the aperture. Aperture with a short, broad, anterior canal. Outer lip with a large, broad, rounded sinus, in front of which the lip projects. Inner lip with callus."

Compared with the type of the genus, this shell is considerably larger; L. 63 mm., D. 18 mm.

TYPE LOCALITY: Cabo Blanco, between Mancosa and Lobitos, N.W. Peru, from the Parinas sandstone of the upper Negritos formation, lower Eocene. "Smaller forms resembling this species are found in the *Turritella* Series" in the lower Lobitos formation. Type in Sedgwick Museum.

?Morgania costata Woods

Woods, *in* Bosworth, 1922:83, pl. 9, figs. 7-10.

Differs from *M. magna* in its smaller size, less tapering apex, but particularly in its compact, irregular, cord-like spirals, with those near the suture somewhat wider; in this last feature resembles *Doryssa,* but the aperture is conspicuously siphonal and more like *Morgania.*

TYPE LOCALITY (and distribution): Same as *M. magna.* Type in Sedgwick Museum.

Family POTAMIDIDAE

Genus *Potamides* Brongniart, 1810

Type: *Potamides lamarcki* Brongniart

= *Eocerithium* Bonarelli, 1927.

Living Potamididae are tropical and subtropical in fresh and brackish-water influenced by tides. The shell of *Potamides* is conical — turreted, with whorls angulate or coronate. The aperture, which is small in relation to shell size, ends in a short canal. The peristome is rather thin and sinuous. The genus differs from *Cerithidea* in several features. It is more scalariform, has deeper sutures, the outer lip of the aperture is less developed, and the siphonal area is simpler. Within the Cerithiacea, *Potamides* is more closely related to the *Aylacostoma* in the Thiaridae, and the sculpture recalls that of the subgenus *Longiverena.*

Bonarelli (1927:95) introduced *Eocerithium* as a subgenus of *Paracerithium* (Procerithiidae), for the species *Chemnitzia potosensis* d'Orbigny, on the basis that d'Orbigny's illustration does not agree entirely with the description. Although it is true that the illustration does not represent the species as it was known to subsequent collectors (it lacks the canal, the sculpture is less marked and the whorls are more convex), illustrations of this very common species in geological papers (for example Ahlfeld, 1946:fig. 47) show clearly the features of the genus. On the other hand, Bonarelli's specimen (1927, pl. 4, fig. 3) is underdeveloped, incomplete, and does not show part of the canal.

Chemnitzia, as used by d'Orbigny in 1839, is now placed as a subgenus of *Turbonilla* with the type, *Melania campanellae* Philippi, by subsequent designation of Dall & Bartsch, 1909.

The habitats of fossil *Potamides* and their ancestors probably were the same as those of the living *Cerithidea,* in muddy, brackish water, and occasionally entirely out of water.

Potamides potosensis (d'Orbigny)

Chemnitzia potosensis d'Orbigny, 1842,3(4):60, pl. 6, figs. 1-3 (under *Melania* on plate).

Eocerithium potosensis, Bonarelli, 1927:95, pl. 4, fig. 13.

Melania potosensis, Brackebusch, 1883; Frenguelli, 1937:310, figs. 84, 85.

Pleurotoma commonensis Fritzsche, 1924:13, pl. 1, figs. 4a-d.

Potamides potosensis, Ahlfeld, 1946:175, fig. 47.

Eocerithium holmbergi Bonarelli, 1927:97, pl. 4, fig. 14.

ORIGINAL DESCRIPTION (parts which disagree with d'Orbigny's illustration in italics): "Shell somewhat elongated. Spire formed by a convex angle (35°) with whorls *grading,* separated by *deep sutures,* ornamented with about ten rather sinuous oblique spiral ribs which are crossed by less prominent axial ones. Aperture oval. Columella simple." (translation). L. 13 mm., D. 6 mm.

TYPE LOCALITY: Santa Lucia Valley, near Potosí, Bolivia. The age of the strata in which it was found corresponds to the upper section of Puca (our Mirafloran), Paleocene. Bonarelli's specimens are from Maimará, N. of the province of Jujuy, Argentina. Those of Frenguelli are from Alemania, province of Salta. Ahfeld mentioned several localities in the "Calcareo-dolomítico" of Bolivia.

E. holmbergi Bonarelli was based on a fragment of *potosensis* which clearly shows the apertural canal.

The location of the type is unknown (not found at the BMNH or the Museum of Paris).

Potamides patagonensis Ihering

Potamides patagonensis Ihering, 1897:315, fig. 20. 1903:209, 222. 1907: 52. 1914:92. Ameghino 1906:54. Windhausen 1918:31, 52. Frenguelli 1930:21, 35, 39, 51. 1953:241. 1953a:336. Feruglio: 1941(1):178, 237, 257, 272, 276, 298.

ORIGINAL DESCRIPTION (translation): "Represented by incomplete specimens with aperture and apex broken. Six whorls (averaging 30 mm.), suture well marked. Each whorl with 5 elevated spiral lines and 14 axial ribs somewhat oblique and nodulus, which disappear at the base of the last whorl. Columella without folds, and the aperture appears to have had a little tooth on the columella; for this reason the species is not a *Cerithidea* as it may appear to be. Collected at 'Lehuen-ark' [Sehuen-Aike]."

The type lot consisted of nine specimens collected by Carlos Ameghino, probably before 1897. The locality "Lehuen-ark," corrected in 1907 to Sehuen-Aike, is in the valley of the Sehuen River (also called Chalia), not far from Mata Amarilla, and the strata belong to the Sehuenan (see discussion on page 21). The type is in MACN.

This species was found in the vicinity of the one *(Potamides chaliana)* discussed in the following section, and I suspect that some of the ref-

erences in the geological literature may not necessarily be *P. patagonensis.*

The sculpture and general features of *P. patagonensis* are so similar to some forms of *Aylacostoma*, especially *Longiverena*, that a revision of better-preserved and abundant materials would suggest its removal from *Potamides* (compare the original figure with that of *A. eucosmius* from Colombia). However, there is great individual variation in specimens of *Potamides* according to age, which is well known in the case of some Pliocene species from Georgia, U.S.A. It should also be noted that the sculpture of *P. patagonensis* very much resembles that of *P. saltillensis* Aldrich, from that state.

Potamides chaliana, new species

Plate 13, figs. 7-9

DESCRIPTION: Shell conic-turreted. Five-and-a-half whorls, slightly convex, grading, imbricating the ones above into the lower; shoulders small, with deep sutures. The last whorl is almost cylindrical in its upper half, becoming rounded at the base. Sculptured with axial ribs (about seven ribs counted in dorsal view) which are prominent at the shoulders, so giving the suture a waved line; the ribs are sigmoid and oblique, with pronounced arch at the middle; between ribs there are very fine lines of growth. Crossed with spiral cords, weaker than the ribs; there are four cords in the penultimate whorl, and about 5 or 6 in the last. The last cord, running from the middle of the columellar area, delimits clearly the basal zone, and below it there are 2 or 3 spiral lines. In some specimens the suture is finely marginated. The aperture is typical of *Potamides*, with a very short canal at the base, slightly twisted to the left. The outer lip in all specimens observed is fractured, but with exception of the basal expansion, the aperture is perfectly circular. In some paratypes the ribs appear stronger, due to partial disintegration of the shell matter in the interspaces.

DIMENSIONS: Holotype: L. 36 mm., D. 15 mm.; aperture (from upper part of columella to canal) 8.5 mm.; inside diameter 6 mm. x 6 mm.; last whorl 19 mm.; penultimate whorl 5.5 mm. Ten paratypes.

TYPE LOCALITY: West side of Amenida Lake at Mata Amarilla on the Sehuen River (also called Chalia), Santa Cruz (Patagonia), Argentina. From strata of the Sehuenan facies of the Jahuel formation. Collected by E. Feruglio, March, 1935. Type in CM.

Although found in the vicinity, and in the same strata, of *P. patagonensis, P. chaliana* differs conspicuously in having sculpture without nodules (which is constant in all observed specimens), a more gradate form, deeper sutures, and larger size.

Potamides turgidus (Bonarelli)

Zygopleura turgida Bonarelli, 1921:70, pl. 9, figs. 1, 2. 1927:54, pl. 1, fig. 1.
Z. paucinodosa Bonarelli, 1921:70, pl. 9, fig. 3. 1927:56, pl. 1, fig. 4.
Z. spinicosta Bonarelli, 1921:70, pl. 9, fig. 6 (not 7). 1927:56, pl. 1, fig. 5.
Z. cossmanni Bonarelli, 1927:57, pl. 1, fig. 7 (*multicosta* in Cossmann).
Z. argentina Bonarelli, 1921:70, pl. 9, fig. 19. 1927:58, pl. 1, figs. 8, 9.
Z. insignis Bonarelli, 1927:58, pl. 1, fig. 10.
Katosira zygopleuroides Bonarelli, 1921:71, pl. 9, figs. 20-21. 1927:63, pl. 1, fig. 13.
K. communis Bonarelli, 1921:71, pl. 9, fig. 24. 1927:64, pl. 1, fig. 16.
K. pseudovetusta Bonarelli, 1921:71, pl. 9, figs. 28, 29. 1927:65, pl. 2, fig. 1.
K. recticosta Bonarelli, 1921:71, pl. 9, fig. 30. 1927:66, pl. 2, fig. 2.
K. carbajalensis Bonarelli, 1921:71, pl. 9, figs. 23, 24. 1927:66, pl. 2 fig. 3.
K. rapidecrescens Bonarelli, 1921:71, pl. 9, fig. 26. 1927:70, pl. 2, fig. 9.
K. clathrata Bonarelli, 1921:71, pl. 9, figs. 36, 37. 1927:71, pl. 2, fig. 10.
K. conoidea Bonarelli, 1921:71, pl. 9, fig. 27. 1927:72, pl. 2, fig. 11.
K brachyspira Bonarelli, 1921:71, pl. 10, fig. 2. 1927:72, pl. 2, fig. 12.
K. obliquicosta Bonarelli, 1921:71, pl. 10, figs. 3, 4. 1927:73, pl. 2, fig. 13.
Rhabdoconcha dubia Bonarelli, 1921:71, pl. 10, figs. 20-21.
Anoptychia sp. Bonarelli, 1927:73, pl. 2, fig. 4.
Hypsipleura (?) *binotata* Bonarelli, 1921:71, pl. 10, fig. 8. 1927:75, pl. 2, fig. 15.
Stephanocosmia disputabilis Bonarelli, 1921:71, pl. 10, figs. 10, 11. 1927:77, pl. 3, fig. 11.
S. frequens Bonarelli, 1921:71, pl. 10, fig. 12. 1927:78, pl. 3, fig. 2.
S. microcantha Bonarelli, 1921:71, pl. 10, fig. 16. 1927:78, pl. 3, figs. 3,4.
S. tyrsoecina Bonarelli, 1921:71, pl. 10, fig. 13 (not 12). 1927:78, pl. 3, fig. 5.
Tyrsoecus andinus Bonarelli, 1921:71, pl. 10, fig. 17. 1927:80, pl. 1, fig. 6.
T. moniliformis Bonarelli, 1921:71, pl. 10, fig. 18. 1927:80, pl. 2, fig. 7.
T. perarmatus Bonarelli, 1921:71, pl. 10, fig. 19. 1927:81, pl. 2, fig. 8.

The name *P. turgidus* [*ida*] selected for this species was the first in Bonarelli's list. The described type consisted only of the last three remaining whorls, with axial costulae worn off, but the angulosity or basal carination of the whorls is well marked. The sculpture can be seen better in the specimen named *K. zygopleuroides*, the best pre-

served, with four whorls and suture clearly marginated. Some forms of this *K. zygopleuroides* have nodules at the base, also seen in those under the generic name *Stephanocosmia*. In a general way, *P. turgidus* recalls *P. chaliana* in sculptural and sutural features, but it is decidedly more cylindrical, with less convex whorls.

Bonarelli based Z. *turgida* and all the other names in its preposterous synonymy on fragments of shells (no complete one is known). The author did not describe these as species but as "forms," and to this term he added "varieties." Both names have been dispensed with in the above synonymy. All species are from the same locality, indicated in the subtitle of the 1927 paper as "Fosiles de Carbajal" from the "Formación Petrolifera" or "Sistema de Salta," thought to be Triassic but now considered Paleocene (see page 197).

Frenguelli, who collected and revised numerous similar fragments from strata of the same age (upper Puca-Mirafloran) of Cerro Colorado, southeast of Santa Victoria, Salta, Argentina (15 miles south of Bonarelli's type locality), declared the impossibility of separating the assumed different forms. He advanced the opinion (1937), to which I subscribe, that all these names correspond to individual variations of a single species of *Potamides*. Except for the form named Z. *cossmanni*, which was figured from a young shell with six preserved whorls, all others are portions of the lower part of shells with costate-nodulous ornamentation of diverse development. Cossmann (1925), who observed Bonarelli's specimens, also expressed his doubts about the taxonomic value of these forms.

? Potamides doelloi (Bonarelli)

Zygopleura (Kittliconcha) doelloi Bonarelli, 1927:60, pl. 1, figs. 1, 2.

It is uncertain whether this form is specifically distinct from *P. turgidus*, the difference being only in the more convex whorls (of the last three preserved) and somewhat smaller aperture. It is from the same type locality as *P. turgidus*.

Bonarelli based his subgenus *Kittliconcha* on a figure from Kittl of *Loxonema walmstedti* Klipst, assigning to it the new name *Kittliconcha cassiana* from the Triassic of Europe. When describing *P. doelloi*, he said that a "comparison between the two forms cannot be made because Kittl's description of the equivalent of *K. cassiana* does not give all the necessary details." Even if *Kittliconcha* has validity, as assumed by Wenz (1938:385, fig. 921), any relationship with the South American *P. doelloi* is untenable.

Potamides decarlesi (Bonarelli)

Zygopleura de Carlesi Bonarelli, 1927:59, pl. 1, fig. 11.

This is the largest, and most peculiar, of the "*Zygopleura*" described by Bonarelli, and it agrees well with *Potamides,* of the *P. mcgilli* stock. The fragment on which the species was described consisted only of the last whorl and part of the penultimate one. The last whorl is twice as wide as the last one in the other species, with the usual ribs transformed into five (in dorsal view) prominent tubercles, below which the base is acutely triangular, with spiral cords. The species has the same type locality as *P. turgidus.*

Potamides mcgilli Pilsbry & Olsson
Plate 17, fig. 6

Pilsbry & Olsson, 1935:9, pl. 1, fig. 1.

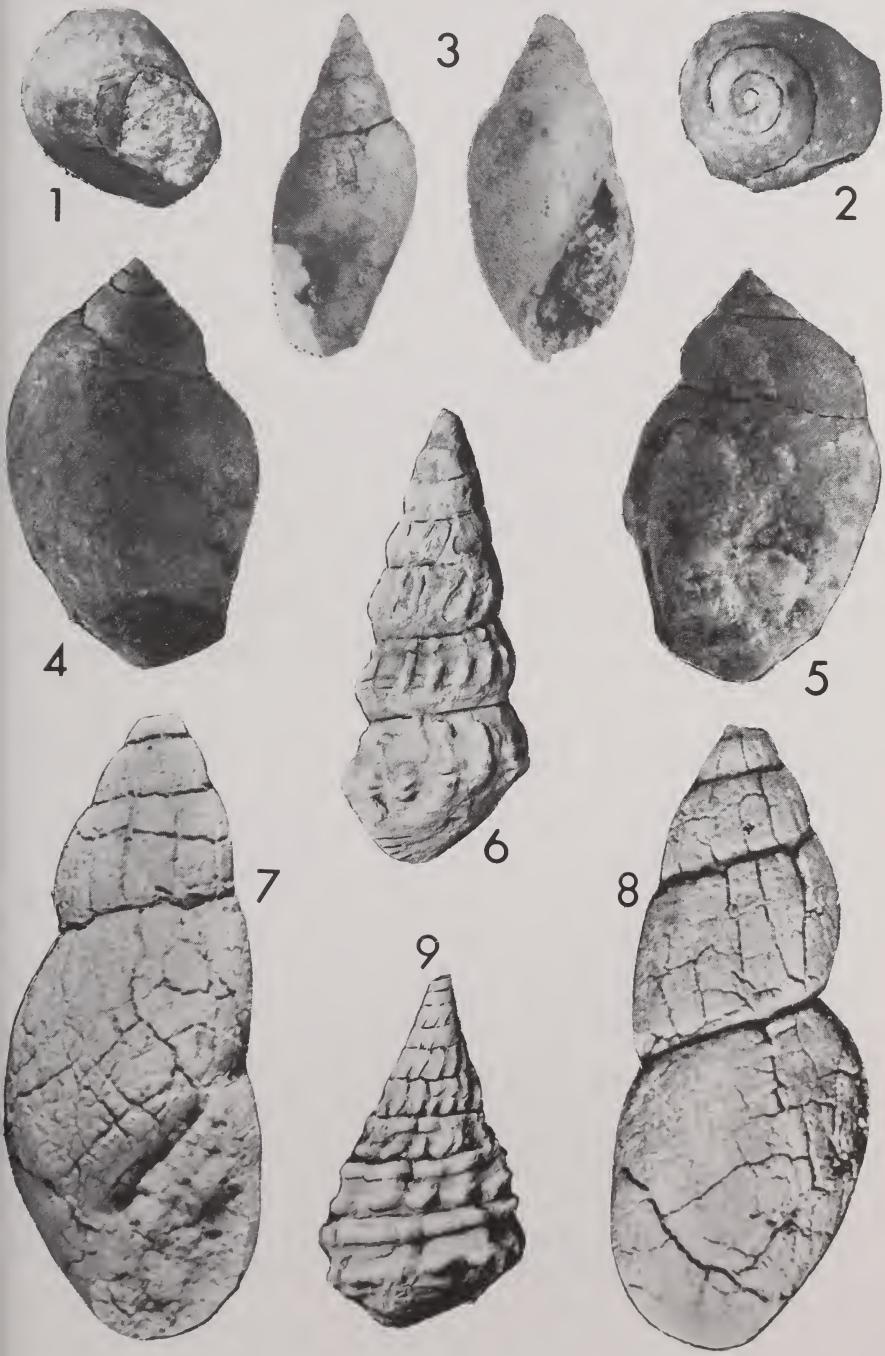
ORIGINAL DESCRIPTION: "The diameter of the turrited [*sic*] shell is contained about 2.6 times in the length. The earlier whorls are only moderately convex, but the convexity increases with growth, the last two being somewhat excavated below the suture, swollen and prominent in the peripheral region. Sculpture of smooth, protractively axial folds on the spire, but on the last whorls, the spiral concavity segregates the upper end of the folds as small tubercles, and three spiral cords appear in the peripheral region, stronger where they pass over the axial folds. The base has about 6 small spiral cords. The inner lip seems to have a rather heavy parietal callus; characters of the aperture otherwise unknown. L. 44 mm., D. 17 mm.; 8 or 9 whorls."

TYPE LOCALITY: Colorado River, Colombia, from Los Corros formation, upper Eocene. Type in ANSP.

The authors referred this species to *Potamides* in a wide sense, the correct generic position being uncertain. It reveals some features like those of *Pachychilus* but shows affinities with *Potamides chaliana* of the Paleocene of Patagonia.

PLATE 17

1,2. *Potamolithoides biblianus* (Marshall & Bowles). Type, x¾.
3. *Chilina stenopstylops* Parodiz. Dorsal (l) and ventral (r) views. Type, x2.
4,5. *Physa doeringi* Doello-Jurado. Type, x1¼.
6. *Potamides mcgilli* (Pilsbry & Olsson). Type, x1.
7,8. *Thaumastus patagonicus* Parodiz. Type, x1.
9. *Diplocyma wheeleri* (Pilsbry & Olsson). x1.


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Potamides occidentalis Woods

Woods, *in* Bosworth, 1922:90, pl. 11, fig. 9.

ORIGINAL DESCRIPTION: "Shell elongate-conical, consisting of numerous flattened or slightly convex whorls, with slightly impressed sutures. Early whorls with three spiral ribs, of which the upper and lower are stronger than the middle rib; subsequently two more small ribs are introduced. The spiral ribs are crossed by folds somewhat oblique to the axis and often in linear series; at the points of intersection tubercules are developed. Last whorl with a rounded protuberance opposite the inner lip; base with several spiral ribs. Aperture broad, with a short, deep, anterior canal and a shallow posterior furrow; outer lip projecting posteriorly, angular in the middle, the posterior part being slightly concave and the anterior part convex and projecting."

No dimensions given; if the illustrations are actual size then the specimen measures L. 41 mm., D. 18 mm., counting the thick expansion of the lip. Its wider conical base, extraordinary development of the outer lip, and larger size distinguish this species from *P. chaliana*, but in the sculpture of the upper whorls the two are very similar.

TYPE LOCALITY: Near Negritos (plus La Brea), N.W. Peru, from the middle portion of the Negritos formation (Clavalithes series), probably in the Eocene-Paleocene transition. Type in Sedgwick Museum.

Potamides lagunitensis Woods

Tympanotomus lagunitensis Woods, *in* Bosworth, 1922:90, pl. 11, figs. 10-12.

ORIGINAL DESCRIPTION: "Shell elongate-conical, whorls flattened, sutures rather deep. Each whorl with two spiral rows of large rounded tubercles, one just below, the other just above the suture. The tubercles of the successive rows tend to be in more or less nearly vertical lines. On the later whorls a fine spiral rib is present in the space between the two rows of tubercles. On the last whorl, just in front of the anterior row of tubercles, are two small spiral ribs. Base of the shell nearly smooth but with growth-lines curving sharply backwards. Aperture not preserved, but a sinuosity in the outer lip is shown by the growth-lines."

No dimensions given, but the specimen in the illustration measures about 40 mm. in length and 15 mm. in diameter. Evidently it is not a *Tympanotomus*. It shows certain affinities with *Aylacostoma* (*Longiverena*), and is much closer to *Potamides* with regular tubercules. Type in Sedgwick Museum.

Potamides suprasulcatus (Gabb)

Cerithium suprasulcatus Gabb, 1873:237.

Potamides suprasulcatus, Jung 1965:490, pl. 64, figs. 11, 12. (Complete references)

This species has been widely revised by Woodring and recently by Jung (1965). It is characterized by its sculpture of three rows (five in

the last whorl) of thick, rounded nodules which covers all the surface except the base, where the nodules become squarish and more compact, forming spiral cords. The sutures are marginated by the row of suprasutural nodules, where they are flat and narrow. There is a tooth-like thickening on the base of the columellar wall bordering a short canal. The inside of the outer lip shows several strong indentations. The shell is of medium size.

P. suprasulcatus is found in northern Venezuela at Pueblo Nuevo in the Paraguana Peninsula, and also at Puerto Lopez, Guajira Peninsula, from middle Miocene beds which mostly contain marine fauna. (Type in ANSP.)

The species resembles *Aylacostoma eucosmius* in its type of sculpture, but in the latter species the nodules are farther separated vertically, the whorls more convex, and the suture deeper. Obviously *P. suprasulcatus* is not related to *Aylacostoma*, but sometimes shell characters in Thiaridae and Potamididae show peculiar convergence. I have not seen this species but I rest on the authority of the revisers cited. Judging from the good illustrations in Jung, the "variety" named *infraliratus* Spieker for *Potamides ormei* Maury, from the Zorritos formation in Peru, does not differ substantially from *P. suprasulcatus* and I do not think that any infraspecific denomination is necessary.

Genus *Lagunites* Olsson, 1929

Type: *Telescopium peruvianum* Woods

This genus is very close to *Potamides*, perhaps only a subgenus consisting of giant shells like *Telescopium* in size, but the spire is not completely flattened-conical, the sutures being more marked and slightly marginated, as in *Potamides*. The sculpture consists of well-separated, thick, axial ribs. The preserved portion of the columella in *L. peruvianus* seems to be of the same type as in *Potamides*, and differs from *Diplocyma*. Except for the basal cords, it does not show other spiral sculpture. The only specimen known has the upper whorls (first five or six) broken away, but the length must have been about 70 mm.

Lagunites peruvianus (Woods)

Telescopium peruvianus Woods, *in* Bosworth 1922:91, pl. 11, figs. 13, 14.

ORIGINAL DESCRIPTION: "Shell conical, consisting of numerous low, flattened whorls bearing many transverse folds [the type shows about 7 in frontal view].

The folds are usually somewhat oblique, but sometimes axial, nearly straight but slightly curved near the anterior suture; on the later whorls the folds are sometimes more distinctly curved. Sutures linear. The periphery of the base is angular, with a deep furrow bounded by a small spiral rib above and by a stronger spiral below."

No dimensions given, but the type (fig. 14) has the later 5 whorls well preserved (except the basal lip), and measures 45 mm. in length and 28 mm. in diameter. The whorls are very regular in size, increasing very slowly from the top. The number of ribs, or folds, is the same in all the whorls, so that in the earlier, smaller ones, the folds are crowded.

TYPE LOCALITY: Lagunitas, 5 miles inland, in S.W. direction from Punta Parinas, westermost Peru. Lobitosan, Eocene. Also "around Negritos and perhaps also Payta." Type in Sedgwick Museum.

Genus *Diplocyma* Pilsbry & Olsson, 1935

Type: *D. wheeleri* Pilsbry & Olsson

ORIGINAL DESCRIPTION: "Potamididae with a smooth early stage, followed by sculpture of somewhat protractive axial folds, which on the later whorls are more or less deeply interrupted, forming two spiral series of tubercles. Last whorl with spiral cords on the base. Lip sinuous, advancing in the lower part; inner or parietal lip heavily calloused throughout. Basal sinus shallow."

This genus appears to be very closely related to *Lagunites*, inasmuch as the immature shells have a rather short, flattened base. It is also related to *Potamides*, with a wider base and acutely tapering spire. Further knowledge may indicate *Diplocyma* and *Lagunites* as subgenera of *Potamides*, but at present the known materials of these groups are very poor.

Two species have been described as *Diplocyma:*

D. wheeleri Pilsbry & Olsson, 1935:10, pl. 2, figs. 2-4. (Plate 17, fig. 9)

D. succionis Pilsbry & Olsson, 1935:11, pl. 2, figs. 5-7.

Both are of about the same size (40-45 mm. long), *D. succionis* differing from *D. wheeleri* by the pronounced tubercles of the later whorls, and slender shape, but the authors indicated other variations in the size and shape of both, especially in *D. succionis.* The specimens of the type species, *D. wheeleri*, are not well preserved. It is not unlikely that the two forms are conspecific.

TYPE LOCALITY: For *D. wheeleri*, mouth of Quebrada Cabezoneras in a branch of the Sogamoso River, Magdalena Valley, Colombia (also at Colorado River). For *D. succionis*, Sucio River, a branch of Llano River, S.E. of Infantas, Colombia. Both from Los Corros formation (Corrosian) Upper Eocene. Types in ANSP.

Order BASOMMATOPHORA
Superfamily CHILINACEA (Hygrophila Thiele, in part)
Family CHILINIDAE

The Chilinidae are primitive Basommatophora, their evolution parallel to the Ellobiidae. The "Prochilinid stock," according to Harry (1964:377), evolved separately from the Ellobiidae, and the "chilinas," which now live in fresh water, began as marine or brackish-water forms. The late Dr. Walter A. Biese of Chile reported that *Chilina fluctuosa* was taken alive in the brackish-water zone of the Gulf of Arauco. The only related family is *Latiidae* of New Zealand.

Genus *Chilina* Gray, 1828

Type: *Chilina fluctuosa* Gray

= *Duplicaria* Rafinesque, 1833.
Ida, Gray, 1836.
Dombeia d'Orbigny, 1836; [*Dombeya* Beck, 1837.]
Potamophila Swainson, 1840.
Pseudochilina Dall, 1870.
Acyrogonia Rochebrune & Mabille, 1889.

This genus is authochtonous to and typical of southern South America. The fossils, as well as the largest of the living species, are found on both sides of the southern Andes, in Chile, and Patagonia. Migration to the east-northeast probably took place during the late Tertiary, and several species are now found in La Plata and the Uruguay rivers as far north as southern Brazil, but not in the tropical areas. This distribution is correlated with that of *Neocorbicula* and *Potamolithus.* Individuals of every species show a wide range of variations in shape and color marks (Note 52).

Chilina (sensu lato) fischeri (Mayer-Eymar)

Actaeonina (Douvilleia) fischeri Mayer-Eymar, *in* Burckhardt 1900:25, pl. 26, figs. 8, 9.

ORIGINAL DESCRIPTION (translation): "Shell ovate-cylindrical. Spire short, apex acute. Whorls almost six, narrow, convex, subangular, last whorl very large, ventricose, attenuated at the base, with longitudinal striae. Aperture large, anteriorly wide and narrowed posteriorly. Columella elongated, narrow. L. 19 mm., D. 15 mm."

TYPE LOCALITY: East of Arroyo Pacunto, affluent of the Bío-Bío River, below Lonquimay River, Chile; from "strata of Lonquimay" synchronic with the upper Concepción formation, upper Paleocene or lowermost Eocene. It was found with *Diplodon, Potamolithus,* and *Ancylus.*

Douvilleia, for which the species was indicated, is actually a subgenus of *Trochaeteonina,* in the Actaeonidae, from the Mesozoic-Cenozoic of Europe. The resemblance to the fossil *Chilina* is in the general shape of the shell, but *C. fischeri* belongs to those species of obese *Chilina,* like *C. ampullacea* Reeve.

Chilina stenostylops Parodiz
Plate 17, fig. 3a,b.

Parodiz, 1963:146, pl. 11, figs. 5, 6.

DESCRIPTION: Shell imperforate, lymnaeiform, spire elongate, very acute, occupying about one-third of the total length. Spiral angle 50°. Penultimate whorl as long as half of the spire, body whorl oval-elongate, narrower at the base, the wider zone at the middle. Suture well marked, with inclination of 12°. Aperture twice as high as wide, very angular above, expanded but narrowly rounded below; columellar margin with a low, slightly developed fold, otherwise thin and straight; basal lip on the left side thick. Length 23.1 - 23.5 mm., diameter 9.7 - 11.7 mm., aperture 12 mm. x 6 mm.

TYPE LOCALITY: Cañadon Vaca, W. of Paso Niemann of the Chico River of Chubut, Argentina. From Casamayor formation, lower Eocene. Collected by G. G. Simpson, 1931. Type in CM.

C. stenostylops has similarities to the group of living species, but its outline is more like that of *Lymnaea,* for which Dall proposed the subgeneric name *Pseudochilina.* It has the same general shape as *C. oldroydae* Marshall without as marked a columellar fold. Probably the columella with many well-developed folds is a feature of more recent species, while the simpler, almost unfolded, parietal wall is a plesiomorphic character.

This is the only fresh-water mollusk known in the Casamayor formation. The other shells present are the land genera *Strophocheilus* and *Thaumastus.*

Chilina antiquata d'Orbigny

D'Orbigny, 1842, 3(4): 114.

This species was never figured. I have not seen any specimen, and apparently it has not been collected since d'Orbigny. That author remarked: "The casts give me the certitude that they belong to *Chilina,* but are incomplete for a description or figure." D'Orbigny found the species at "Barrancas al Sur" on the right margin of the Negro River in Patagonia, in the same beds with *Diplodon diluvii,* which is a Pliocene form. (Type location uncertain.)

Superfamily LYMNAEACEA
Family LYMNAEIDAE
Genus *Lymnaea* Lamarck, 1799

Type: *Helix stagnalis* Linnaeus

The fossil shell of this family, described below, is slender with a weak columellar fold as in *Stagnicola*. The subgenus *Stagnicola*, however, is not known south of the equator, and taxonomists held different opinions about its systematic position or validity: for some authors there exists only a single genus, *Lymnaea*. And others consider *Stagnicola*, *Fossaria*, and *Pseudosuccinea* as subgenera, or as distinct genera.

Lymnaea klappenbachi, new species
Plate 11, fig. 5

DESCRIPTION: The shell was metamorphosed into chalcedony, well preserved except for the basal portion of the lip, which appears to have been twisted to the left (a feature common in *Stagnicola*). The lip is sharply expanded toward the front at the superior angle, where it is very lightly detached from the body whorl. The spire is about one-third of the length of the last whorl and is slender. Last whorl rounded at the base. Columella with a weak twist at the middle. L. 22 mm., d. 10 mm., aperture 11 mm. x 14 mm. Complete, with the lip entire, it must have been 24 mm. long and the last whorl 16 mm.

TYPE LOCALITY: Sandstone of Palmitas, Department Soriano, southwest Uruguay, from the strata of Fray Bentos (="Palmirense"). Collected by A. Berro, 1927: three paratypes. Type in CM.

Fossils of the Fraybentosan were formerly associated with the Senonian, but the "Palmiran," according to G. G. Simpson (1940), is almost contemporaneous with the Friasean, and the "Palmirense" of authors corresponds to the Fray Bentos beds (Miocene). This is discussed in Note 18. In certain locations, the eroded Fray Bentos beds appear lying directly over the Asencio sandstones (Cretaceous), and this may account for the condition of the fossils. These data, however, do not exclude the possibility that *L. klappenbachi* is older, perhaps Queguay (see comments on *Taphius walteri*). The case is probably similar to that of the problematic "*Bulimus* sp." mentioned by Caorsi & Goñi, 1958:56.

One of the two paratypes is of the same shape but smaller than the type. A larger one, not crystallized, of which only a fractured body whorl remains, is 20 mm. long.

The species is named for Dr. Miguel A. Klappenbach, leading Uruguayan malacologist and curator at the Museum of Montevideo.

Limnaea klappenbachi may belong to *Stagnicola*. As this is the only fossil *Lymnaea* known from South America, better materials will be needed to clear up its subgeneric status.

Family PLANORBIIDAE
Genus *Taphius* H. & A. Adams, 1855

Type: *Planorbis andecolus* d'Orbigny
= *Tropicorbis* Pilsbry & Brown, 1914.
Platytaphius Pilsbry, 1924.
Australorbis Pilsbry, 1934.

In recent years the name *Biomphalaria* has been used instead of *Taphius*. In 1961 F. S. Barbosa, B. Hubendick, E. T. A. Malek, and C. A. Wright concurred in conclusions of previous research by Hubendick that "on anatomical evidence the planorbid genera *Australorbis*, *Biomphalaria*, *Platytaphius*, *Taphius* and *Tropicorbis* are not distinct, and should be united into a single genus, "These authors also added that "there is no doubt that *Taphius* is the oldest name and should take priority" (ibid.:372). But after discussing the availability of *Taphius* conflicting with *Planorbina* Haldeman, 1842, they suggested the adoption of *Biomphalaria* Preston, 1910, because medical parasitologists and health workers "would be most affected by changes" [to *Taphius*]. The International Commission on Zoological Nomenclature, attending to such arguments, ruled (1965 Bulletin 22(2):94) *Biomphalaria* to be the valid name. This hasty decision was not only entirely arbitrary, made against the law of priority, but also disregarded the Commission's own recommendations for conserving names with more than 50 years of general use. *Taphius* had been used for 110 years and was introduced 55 years before *Biomphalaria*. Furthermore, the authors cited by the Commission in support of the rule were not all consistent: the previous year (1964) Hubendick (himself) and Harry (1964:42) had declared that the genus "*Taphius* is presently recognized as the only one in the [Taphiinae] family." Regarding the alleged precedence of *Planorbina* Haldeman, 1842, the status of that name had been clarified by Pilsbry (1934) and F. C. Baker (1945), and Dall's selection in 1905 of *Planorbis olivaceous* Spix as type was wrong, since Haldeman was referring to a European species, *Planorbis spirorbis* Linnaeus.

If disregard of the International Code in favor, or for the convenience, of any non-systematic group of workers is accepted practice, then taxonomists will face the dilemma of having to choose between

the authority prescribed in the Code and arbitrary decisions outside the rules.

Taphius walteri, new species
Plate 18, fig. 1

"*Planorbis walteri* Ihering" *in litteris* of authors.

DESCRIPTION: A well-preserved specimen with only a small part of the last whorl around the peristome broken. Five whorls separated by well-impressed suture. The false umbilicus is deep, almost perspective. The whorls increase rapidly in size, and the end of the last one is almost as wide as the four preceding ones, and a little higher. The shell is perfectly circular, both major and minor diameter being equal: 10 mm. The altitude of the whorls, not carinated but perfectly convex, is 9.5 mm. This species is very close to *T. peregrinus* d'Orbigny, but with the earlier whorls very narrow and flat.

TYPE LOCALITY: Palmitas. S.W. Uruguay, in the same strata with *Lymnaea klappenbachi.* Coll. A. Berro, 1927. Type in CM.

This is probably the same species which Walter, and Caorsi & Goñi (1958:56) referred to as "*Planorbis walteri*" Ihering, from the "Calizas de Queguay," Oligocene, in the Department of Durazno, Paysandu, and Canelones, but our described type is from Soriano, in the so-called "Palmirense." *Planorbis walteri* was never described or figured and is a *nomen nudum,* but I preserved that specific name for the new species as it appears in the geologic literature.

Taphius molino (Pilsbry)

Planorbis molino Pilsbry, 1939:70, pl. 9, fig. 3. Ahlfeld, 1946: pl. 7.

ORIGINAL DESCRIPTION: "Small species, deeply concave on both sides, the concavity of the left side a little narrower. It is composed of about three, rapidly enlarging, cylindric whorls. The aperture is only slightly oblique, relatively large, its outline circular, about 1/7 of the circle excised at the contact with the preceding whorl. The shell appears to be smooth, but as no lines of growth are apparent, the surface features may not be perfectly preserved" (Pilsbry). D. 2.3 mm.; height at the middle of last whorl (half-whorl from aperture) 8.75 mm. Another specimen: D. 1.5 mm., H. of aperture 8.75 mm.

TYPE LOCALITY: El Molino, near Potosí, Bolivia. Strata of upper Puca (Mirafloran), Paleocene. (See *T. boliviensis*). Type in ANSP.

?*Taphius monserratensis* (Hartt)
Plate 15, fig. 7

Planorbis monserratensis Hartt, 1870:351.
Planorbis (*Gyraulus*) *monserratensis*, White, 1887:239, pl. 26, figs. 16-18.

ORIGINAL DESCRIPTION: "Shell very small, discoid; volutions three or three and a half in number, so rapidly increasing in size that the diameter of the last one near the aperture is nearly equal to one half of the full diameter of the coil; transverse section of the outer volution subcircular in outline; upper side of the coil nearly flat, or even a little concave; suture impressed; under side of the coil deeply and broadly umbiculate; surface plain. Diameter of the coil, 3.5 mm.; diameter of the outer volution at the aperture 1 3/5 mm." (White-Hartt).

TYPE LOCALITY: Monserrate, 10 km. N. of Bahia, in the lacustrine deposits filling the eroded surfaces of the Bahia Series, Paleocene.

This small planorbid seems to have a rather thick peristome. The shape of the aperture is oval, subangulated on the parietal side. As identification of a species can be correctly done only by examination of soft parts, the assignment of this fossil species to *Taphius* is based on similarities of its shell to *T. peregrinus* (d'Orbigny). (Type location uncertain. Original collection examined by Dr. White was from MNRJ.)

"Planorbis" pebasana Conrad

Conrad, 1874:30.

ORIGINAL DESCRIPTION: "Discoid, depressed, volutions 3, convex, channelled along the suture, glossy, base concave, volutions rounded, separated by a deep channel; aperture round." (Conrad).

No illustrations given, and the diagnosis is insufficient to identify the species. It may be the same as *"Planorbis bouguyi"* Roxo from the Javary River at Tres Unidos, Amazonas, Brazil, and most likely Pleistocene. According to some specimens observed from this locality, *P. bouguyi* is not planorbid but some minute helicoid snail.

TYPE LOCALITY: Pebas, Peru, in the Iquitos region. If it was taken *in situ* from the strata it may be a Pliocene shell, but Conrad remarked that it was very fresh, "looking a living [one]." Type in ANSP.

?*Taphius boliviensis* (Fritzsche)

Planorbis boliviensis Fritzsche, 1924:24.

This is an unfigured species with no outstanding characteristics useful for comparison. The locality is Miraflores, in the upper Puca formation of Bolivia, Paleocene. It may be co-specific with *T. molino*. (Type location assumed to be NR, where the original collection was deposited.)

Family PHYSIDAE
Genus *Physa* Draparnaud, 1801

Type: *Bulla fontinalis* Linnaeus

= *Exydra* Ferussac, 1821.
Rhyza Risso, 1826.
Rivicola Fitzinger, 1833.
Echemytes Gistl, 1848.

Physa wichmanni Parodiz
Plate 19, figs. 9-11

Parodiz, 1961: 1, figs. 1-3.

DESCRIPTION: Shell medium sized, rimate (fissure very narrow), elongate-ovate. Widest diameter is 1.95 times total length. Six and one-half whorls, the last occupying almost ¾ of the length. Suture not marginated but well marked, with inclination of 23°. On the last whorl the surface shows rather strong and very regular growth lines. It also presents a dark-banded zone, which occurs in some living species. Aperture elongated, rounded at the base, with columellar margin straight and a little expanded. The interior of the shell is filled with tuffaceous matrix.

DIMENSIONS: L. 15.6 - 19 mm.; major d. 8 - 10 mm.; minor d. 7.8 - 8.5 mm.; last whorl 12.3 - 14 mm; number of whorls 6½ - 7; sutural angle 23 - 26°

TYPE LOCALITY: Bajo Santa Rosa, 50 miles S. of Negro River at Chelforo, province of Río Negro, Argentina, from the Jahuel formation (Danian), collected by R. Wichmann, 1915. Type in CM.

Except for a small broken portion of the peristome, the holotype is very well preserved, with the tip of the protoconch complete, and partly crystallized by infiltrations of silica. Two other specimens are from the same strata but another locality: Nahuel Niyeu, near Valcheta. One of them is smaller, with the columellar lip submarginated, and the surface with strong and regularly spaced costulae-like lines of growth. The other, larger, is flattened and distorted by diastrophic pressure, a condition common to many fresh-water shells found in the same formation.

This and the following species were found in the same localities with *Diplodon bondenbenderi, Potamolithus windhauseni, Lioplacodes wichmanni,* and *Paleoanculosa bullia.* At the end of the Paleocene, *Physa* (and other coeval genera) disappeared from the region, but were found again to the north in the Pliocene-Pleistocene strata. It is presumable that the living South American species derived from a stock of modern northern migration, rather than from the old Tertiary species.

Physa doeringi Doello-Jurado
Plate 17, figs. 4, 5.

Doello-Jurado, 1927:411, pl. 11, fig. 76. Parodiz, 1961a:1, figs. 7, 8.

This is a gigantic and very inflated form, with only five whorls, more than twice as large as *P. wichmanni*, and in relation to its diameter the spire is very short. The general shape of *P. doeringi* recalls the African *Physopsis* of the Planorbiidae, but the anatomical features that differentiate these groups cannot be detected in fossils. For paleogeographical reasons *doeringi* is, with the greatest likelihood, a *Physa*.

DIMENSIONS: L. 13.8 - 38 mm.; major d. 8.5 - 27 mm.; minor d. 7.5 - 23 mm.; last whorl 30 mm.; sutural angle 10 - 15°. Ratio, length/major diam. for three different localities: Trapalco, L, = 1.49:1; Santa Rosa L. = 1.29:1; Nahuel Niyeu, L. =1.72:1.

TYPE LOCALITY: Trapalcó, in Bajo de los Menucos, (a southern continuation of the lowlands of Santa Rosa), Río Negro; also at Nahuel Niyeu, in same strata as *P. wichmanni*. Type in CM.

Family ANCYLIDAE
Genus *Paleoancylus* Yen, 1948

Type: *P. radiatus* Yen
Paleocene (Fort Union) Montana

?*Paleoancylus humboldti* (Mayer-Eymar)

Ancylus humboldti Mayer-Eymar, *in* Burckhardt, 1900:24, pl. 26, figs. 12-14.

DESCRIPTION: The original diagnosis of this species is very short (translation): "Shell small [perhaps juvenile], conic, base ovate-rounded, apex central, acute, concentrically laminated, with irregular ornamentation. D. 4.5 mm., H. 3.5 mm."

TYPE LOCALITY: A single specimen, from East of Pacunto, Bío-Bío Valley, Chile, in strata with *Potamolithus capitatus* and *Diplodon burckhardti*.

The generic position of this species is uncertain, and its reference to *Paleoancylus* is only tentative. As in *P. radiatus* the shape is almost perfectly conic. *P. radiatus* has a sculpture of grooved lines from the apex to the base, but in *P. humboldti* the sculpture is circular, as in *Rhodacmea*. It may represent a genus different from all the known living ones, but our knowledge of this form is so poor that no conclusions can be reached.

Order STYLOMMATOPHORA
Suborder SIGMURETHRA
Superfamily CLAUSILIACEA
Family CLAUSILIIDAE
Subfamily NENIIANAE
Genus *Cirrobasis* Conrad, 1874
Cirrobasis venusta Conrad

Conrad, 1874a:31, pl. 1, fig. 5 (monotype, Zilch).

The indication of *Cirrobasis* as Clausiliidae is from Zilch (Wenz, 1960:410, fig. 1465). Very little is known of this genus and species, of which only one specimen was known. Although Conrad indicated its origin as the Pliocene of Peru, in the Pebas formation, it may not be a true fossil.

Superfamily STROPHOCHEILACEA
Family STROPHOCHEILIDAE

Thiele's (1926) Strophocheilidae has been also indicated as a subfamily of Acavidae. Most authors include the family within the Acavacea but H. B. Baker referred it to the "Cerionoidea" (1956, 69:135). Subsequently the same author placed Dorcasiidae and Strophocheilidae in the Mesurethra, and Acavidae in the Holopoda, a subdivision of Sigmurethra. Here the family name is used in the sense of Taylor & Sohl (1962:11,19). The similarities to the African Acavidae are due to parallelism or convergence. The shells of *Burtoa* (Achatinidae) from tropical Africa bear extraordinary resemblance to *Strophocheilus*. All Strophocheilidae, *sensu lato* (tribe Strophocheilini), are exclusively Neotropical, living and fossil, and the family may be considered autochthonous to southern South America, where it is found in the very early Tertiary. Many species are of very large size, and Bequaert (1948) recognized two genera and seven subgenera with 50 species, some of them quite variable, divided into "races" or subspecies.

Genus *Strophocheilus* Spix, 1827

Type: *Strophocheilus almeida* Spix
= *pudicus* Müller

= *Otis* Ferussac, 1821, not Linnaeus, 1777.
Strophochilus Agassiz, 1846.
Coniclus Albers, 1850.

Strophocheilus chubutensis Ihering

Ihering, 1904:241, pl. 2, figs. 13, 14; 1907b:463; 1914:70.
Bequaert, 1948:48. Parodiz, 1949a:181, fig. 1a.
S. (*Megalobulimus*) *chubutensis*, Parodiz, 1946a:308.

The original description of *S. chubutensis* follows (translation):

"Shell ovate-oblong, imperforated, spire short acuminate, five or six whorls almost flat, suture slightly deep. Outer lip thick, reflexed; inner lip adhered to the adjacent portion of the shell. Aperture rather small, less than half of the total width of the shell. L 58 mm., major D 27 mm., aperture 25 x 15 mm. Locality: Cañadon Blanco between the rivers Senguerr and Chubut."

Besides the locality indicated above Ihering also made reference to another in the Chico River. Actually these represent two different species. The problem of which of these two lots contained the true type of the species was obscured by Ihering himself, who in subsequent publications reversed the references. After a revision of the lots, and evaluation of the diagnosis, dimensions, and illustrations, it appears that the type of *S. chubutensis* is from Cañadon Blanco. In its lot there are twelve "cotypes" (casts), one of them illustrated and selected as the type (Parodiz, 1949a). In the Catalogue of 1914, however, Ihering had designated as type (in this case "syntypes") the three specimens from Río Chico that never were figured or measured, indicating (in Ihering's handwriting) on the label that they were collected by Hauthal. But another label names C. Ameghino as the collector. To this it must be added that the lots from Cañadon Blanco and Río Chico, are both marked "type" with the conventional sign Ihering used for that purpose. Thus there were three specimens from Cañadon Blanco and three from Río Chico called "types." This confusion was resolved by selecting the specimen illustrated by Ihering on plate 2, fig. 14 as type. In the Argentine Museum collection at Buenos Aires there are also 14 paratypes (from Ihering's original collection) plus three specimens of the same lot F. Ameghino reserved for his own collection before sending the materials for study to Ihering. It should be noted that the specimens of the Chico River belong to the species *S. hauthali* of the subgenus *Megalobulimus*.

TYPE LOCALITY: Cañadon Blanco is a westward continuation of the cliff south of Lake Colhue Huapi, with several early Tertiary strata, especially the Casamayoran, from which a rich fauna is known. The age of *S. chubutensis* is then lower Eocene, which corresponds to what Ihering indicated as "formation of *Notostylops*" and "*transición del Cretáceo al Terciario*" (Ihering 1904:239), included by most authors at that time in the upper Cretaceous. Type in MACN.

Ihering remarked that the species "is represented by poorly preserved casts." I have observed that these casts are not as badly preserved as this might imply; in several of them the upper whorls are complete. Still preserved in the type is part of the shell adhered to the cast. The shell is thin, with wrinkles of growth. The thinness indicates that there probably was not much difference in size between the casts and the actual shell.

Strophocheilus sanctijosephi [sancti-josephi] Maury (Note 42).
Plate 19, figs. 1, 2

Maury, 1935: 7, figs. 8, 9. Parodiz, 1949a: 183.
S. (Microborus) sanctijosephi, Bequaert, 1948:175.
S. (S.) charruanus (in part), Klappenbach & Olazarri, 1966:233.

ORIGINAL DESCRIPTION: "Shell rather large, and broadly ovate in form. Early whorls not preserved but the shell when entire included 7 whorls. The surface is much worn and eroded, but in a few small areas fine, oblique wrinkles of growth are preserved and the entire surface was probably similarly striated. Aperture narrowly oval. Estimated langth of complete shell 45 mm., greater width 27 mm., length of aperture measured obliquely 24 mm., width 10 mm. Although poorly preserved this shell is so unlike any associated species in the limestone [of Fazenda São Jose] that it can be easily recognized by its broad ovate form and comparatively large size. It was judged by Pilsbry to be a new species."

TYPE LOCALITY: Fazenda São Jose, Municipality of Itaborai, Río de Janeiro, Brazil. In a pure, light-yellow limestone. Types in AMNH.

The age originally given by Maury was "probably Miocene with an extreme upper limit of Pliocene." But the Itaborai fauna (vertebrates) contains fossils of different ages from Paleocene to Pliocene. Paula Couto described mammals (Condylarthra) coeval with fossils of the Riochican in Patagonia (Paleocene), and Simpson described others (Didelphiidae) from the same locality of probably Casamayor age (Eocene). E. A. Martins also referred (1959:43) to this "*bacia calcaria de São Jose de Itaborai com moluscos — Strophocheilus — de idade paleocena.*" Trindade (1956) arrived at the same conclusion. All the other fossil mollusks found at Itaborai, *Bulimulus, Itaboraia, Brasilinnea*, are probably Miocene-Pliocene, as Maury, and Oliveira & Leonardos (1943) indicated.

Although this poorly known fossil is smaller than the regular species of the subgenus *Megalobulimus*, it is still too large (the full shape of the lip is unknown) to be an *Austroborus*. Here it is placed within *Strophocheilus, sensu lato.*

Strophocheilus charruanus (Frenguelli)
Plate 18, fig. 2

Borus charruanus (Doello-Jurado) *in litteris, in* Frenguelli, 1930b:24, figs. 5b, 6b.
Strophocheilus atavus Bequaert, 1948:47, pl. 8, fig. 3.
Bulimus archiplatae Ihering, in Walther, 1931: 35. *Nomen nudum.*
Strophocheilus charruanus (Frenguelli), Klappenbach and Olazarri 1966:234 (see Note 59).

The name *charruanus* was originally indicated without a description, but was well defined by Frenguelli (1930b), based on numerous specimens from the Miguez limestone (Dept. Canelones, Uruguay). That author added that "*B. charruanus* does not correspond either to the Patagonian types [of *Strophocheilus*] or the *Borus* which is often collected in the lower pampas of the Uruguayan valleys (= *S. globosus* and *S. lutescens*)." Although this indication is meager, it is supplemented by good photographs of the specimens of *B. charruanus* as well as of other species implied in the comparison, and as the illustrations bear the legend "*Borus charruanus,*" it satisfies the requirements of Article 12 (names published before 1931) and 16 of the ICZN for the purpose of priority. The synonym *S. atavus* sent to Bequaert by F. Felippone, from the same locality and strata, was fully described as follows:

"Shell medium sized, ovate in outline seen in front, widest about mid-length, the spire more tapering than the base. Whorls 5, separated by shallow sutures, that of the body whorl seen from the back more oblique than the one above it. Spire very short, obtusely pointed, as now preserved (the early whorls being preserved only as inner casts, the spire was probably longer). Body whorl moderately convex, shaped much as in *S. erythrosoma,* somewhat saccate at the base to the left of the columella, moderately flattened dorso-ventrally, its upper terminal portion slightly depressed behind the outer lip. Aperture (as preserved) semi-elliptical; parietal wall heavily calloused, about as long as columella; outer lip expanded (rim mostly lacking); columella nearly straight, much widened and flat near the parietal wall, the outer edge overlapping the well-pronounced umbilicus, which was probably openly rimate, the base evenly rounded into the outer lip. Nepionic sculpture unknown (shell material lacking from early whorls). Penultimate and body whorl with the shell material mostly preserved, showing moderately spaced, regular growth-striae and here and there what may be traces of spiral raised lines divided into granules. The shell is completely filled with a hard, compact, white, calcareous matrix." L. 43 mm., width in front view 28 mm., width in profile 23 mm., aperture L. 24.5, width 12.5 mm.

TYPE LOCALITY: Miguez (65 km. N.E. of Montevideo), Departamento Canelones, southern Uruguay, in the Miguez limestone, corresponding to the Queguay forma-

tion, Oligocene [which is the oldest Tertiary known in Uruguay resting on the eroded surface of the Asencio sandstone (Cretaceous)]. The materials I examined from the type locality belong to three lots:

One specimen in matrix, complete, approximately equal in size to the type of *S. atavus*, showing perfectly the large aperture with thin lip, collected by Frenguelli in 1929, belonging to the type lot.

Two specimens collected by Terra Arocena in 1929; one of them complete and well preserved. Filled with hard matrix, but the portions of the shell adhered to the matrix are very thin, no more than 1 mm. thick.

Eight specimens collected by A. Tremoleras in 1923, some of them complete.

The preserved portions of the shells show conspicuous, very regular and widely striated sculpture, especially strong below the suture, and faint, interrupted spirals. The nepionic whorls are almost smooth although some axial lines are visible. The species is regular in size, most specimens approaching that of *S. atavus*, but a larger one is 50 mm. long and 32 mm. wide.

Doello-Jurado, who received the first specimens from Tremoleras in 1923, sent some to Ihering for inspection which were returned without identification or comments. But meanwhile Ihering had written to Walther communicating a new name for similar materials. The latter author in his paper of 1931 (and Lambert, in 1939) mentioned it as "*Borus archiplatae* Ih." which is a *nomen nudum*.

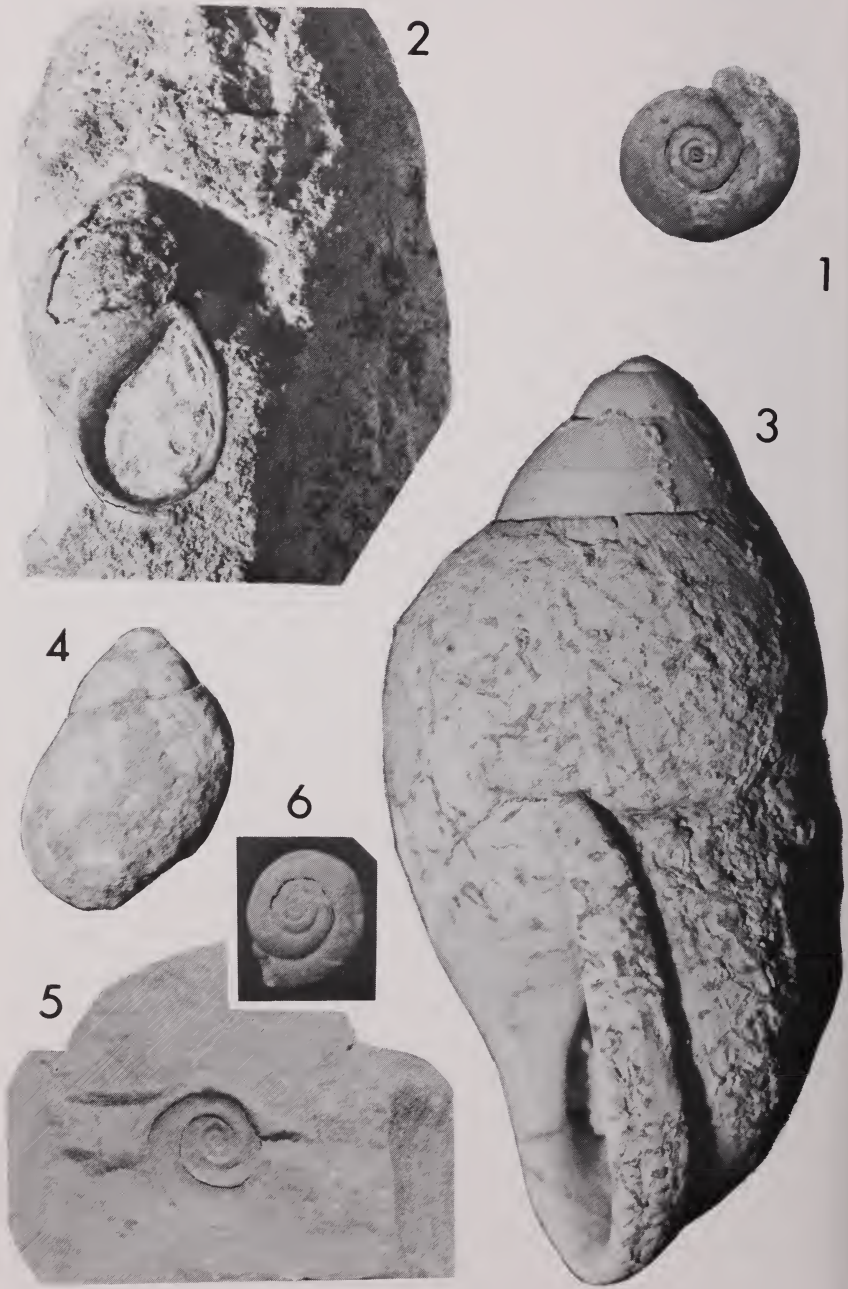
As Bequaert and Frenguelli indicated, this species is certainly different from any of the *Strophocheilus* known from the Eogene of Patagonia, or those living today in Uruguay. Bequaert thinks it is close to *S. erythrostoma*. It also has some resemblance to *S. cordillerae*, a living but almost extinct species of central Argentina, in Córdoba, but the latter form is shorter and belongs to the subgenus *Austroborus*. The closest relationship, however, may be with *S. sanctipauli*, which is almost of the same size but more globose.

The type in Frenguelli's original collection was in La Plata Museum.

Strophocheilus globosus (Martens)

Bulimus globosus Martens, *in* Pfeiffer, 1876, Monograph. Helic. :8:17.
Strophocheilus felipponei Ihering, 1928:96.
Strophocheilus (Megalobulimus) globosus, Bequaert, 1948:142, pl. 4, fig. 7; pl. 15, fig. 2; pl. 20, fig. 2. Parodiz, 1949b:280.

I have seen Pleistocene but not Tertiary fossils of this species, but Caorsi & Goñi (1958:58) stated that was found in the upper portion of the Fray Bentos limestone (Miocene), northeast of Mercedes, Uruguay. However, these authors expressed uncertainty about the age of these strata. This well-known living species is very common in the western


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1
3
4
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section of Uruguay, and its type locality is Montevideo. Pleistocene specimens are known from Entre Ríos and Buenos Aires provinces in Argentina.

Subgenus *Megalobulimus* Miller, 1878

Type: *Bulimus popelairianus* Nyst
= *Borus garciamorenoi* Miller

= *Bulimus* Scopoli, 1786, not 1777.
Borus Albers, 1850, not Agassiz, 1846.
Corus Jousseaume, 1877.
Megalobulimus Haas, 1935.
Streptocheilus Souza Lopez, 1940.
Lophocheilus Daniel, 1942.
Phaiopharus Morretes, 1952.
Psilocus Morretes, 1952.

This subgenus includes the largest species of the family, some reaching 150 mm. in length. In many old collections the species are often found labeled as *Borus*. The range of the living species is from the Island of Trinidad, facing the Orinoco delta of Venezuela, south to central Argentina in the provinces of San Luis, Córdoba, and Entre Ríos.

Strophocheilus (Megalobulimus) hauthali (Ihering)

Strophocheilus hauthali Ihering, 1904:240, pl. 2, fig. 12; 1907b:463; 1914:70. Ameghino, 1906:83.
S. *(Megalobulimus) hauthali,* Bequaert, 1948:119. Parodiz, 1949a:183.
S. *(Megalobulimus) avus* Parodiz, 1949a:181, fig. 1b.

DESCRIPTION: The original lot of this species was collected by Carlos Ameghino at the same time (1899) and from the same strata as *Strophocheilus chubutensis.* The type has six whorls, with deep suture, and shows vestiges of strong longitudinal costulae or lines of growth. The lip is thick and reflexed. The parietal callus

PLATE 18

1. *Taphius waltheri* Parodiz. Type, x3.
2. *Strophocheilus charruanus* (Frenguelli), in silicified marl matrix. x1¼.
3. *Strophocheilus oblongus haemastomus* (Scopoli). x1¾.
4. *Strophocheilus lutescens dorbignyi* (Doering). x1½.
5. *Epiphragmophora feruglioi* Parodiz. Cast of the type in the red clay of the "Subandean Tertiary." x1.
6. *E. feruglioi* Parodiz. Type, x1.

appears as an obtuse tubercle. Aperture oval and subangulated above. L. 98 mm., major d. 55 mm. (56.1% of total length), aperture 45 mm. x 28 mm.

TYPE LOCALITY: Cañadon Blanco, Chubut. The type lot contains four specimens, but the only well-preserved one is the type, which is in MACN.

Another lot was collected by C. Ameghino (also in Ihering's collection), from Colhue Huapi, in the "Capas con *Astroponotus*," Mustersan (upper Eocene).

As in the case of *S. chubutensis*, the collector of the type lot was C. Ameghino (the labels bear his handwriting), not Hauthal as Ihering indicated or as the name of the species may suggest.

When I revised numerous populations of *S. oblongus* and allied species and subspecies, the great variability of the forms sometimes proved to be very confusing. Considering such variability the species I described in 1949 as *Strophocheilus avus* (on materials separated from the lots of *S. chubutensis*), is in all probability a synonym of *S. hauthali*, the type corresponding to an individual of large size. The type locality of *S. avus*, collected by C. Ameghino in 1899, was Río Chico, in the upper strata of Casamayor. The differences between *S. avus* and *S. chubutensis* were approximately the same as those between *S. chubutensis* and *S. hauthali*. The only difference between *S. avus* and *S. hauthali* was the size, the major diameter of *S. hauthali* being about five per cent larger than that of *S. avus*.

The locality "Río Chico, Chubut," indicated in many of the labels of Burmeister, C. Ameghino, Ihering, Roth, Hauthal, and other collectors, was a general reference to a place in which various strata of different ages are found. The typical "Río Chico" formation would be Ameghino's "*Notostylopense basal*," but neither G. G. Simpson (who clarified the stratigraphy) nor any other investigator indicated that *Strophocheilus* were found together with the earliest mammal fauna of the Riochican. Most geologists made references to finding "*in situ*" *Strophocheilus* in the Notostylops (not "*basal*") beds, that is, the Casamayor formation. Feruglio (1949, 2:49, fig. 101 map), indicated "*Capas con Strophocheilus*" in the center of Cañadon Hondo (north of Pampa del Castillo), about four or five miles southeast of Río Chico. Cañadon Hondo, according to Simpson (1948), is "a major locality for the Riochican fauna and also includes unusual variety of Casamayoran facies."

Strophocheilus (Megalobulimus) oblongus haemastomus (Scopoli)

Plate 18, fig. 3

Bulimus haemastomus Scopoli, 1876, 67, pl. 25, fig. B1, 2.

Bulimus (Borus) oblongus crassus Albers, 1850:142, 144.
S. (Megalobulimus) oblongus haemastomus, Bequaert, 1948:74, pl. 2, fig. 2; pl. 21, fig. 4; pl. 24, fig. 5. Parodiz, 1949b:217.
(For complete synonymy and references see Bequaert, 1948.)

This is the form usually referred to in the literature as *B. crassus*, characteristic of the southeastern portion of the species range, especially the province of Entre Ríos in Argentina, extending northeast into Uruguay and southern Brazil. It should be noted however that, although morphologically distinct, its allopatry is not defined sharply enough to qualify it as a valid subspecies. Its distribution overlaps in part that of other subspecies differentiated by Bequaert, who remarked (1948:9) that "all forms below the level of species have been given the status of subspecies or races, although it is realized that they do not all have the same taxonomic value."

The characteristic by which *S. haemastomus* is most easily recognized is the extraordinary thickness and width of the folded outer lip and the heaviness of the very solid shell, especially in gerontic specimens. But specimens with a less developed lip are found occasionally, while some populations of typical *S. oblongus* may have a thick lip. Bequaert thinks that lip development in *S. haemastomus* results from ecological conditions, plus individual age, and its taxonomic evaluation presents a problem. If so, such conditions are not restricted to the Recent because shell of the middle Tertiary (in the same area) show similar characteristics. In any event, typical *S. oblongus* is rarely found in areas where *S. haemastomus* is abundant.

Ihering (1907b:464) referred to *B. crassus* from the Entre Ríos formation at Paraná, but the identification might have been doubtful on account of poor preservation of the fossils. But I have at hand a perfect specimen, from Uruguay, with a folded lip about 8 mm. wide and 3 mm. thick, which is an unmistakeable *S. haemastomus*, collected by Doello-Jurado in 1914 in the ravine near Arroyo Yaguarete Chico, near Fray Bentos, of Miocene age (Note 53).

Subgenus *Austroborus* Parodiz, 1949

Type: *Bulimus lutescens* (King & Broderip)

= *Microborus* Pilsbry, 1926 (not Blandford, 1897).

This group contains species of very small size and occupies the southernmost portion of the family range, in Uruguay and the southern

sierras of the Buenos Aires province, with a west-northwest extension into Córdoba, where a single species, S. *cordillerae*, almost extinct, is known.

Strophocheilus (Austroborus) lutescens dorbignyi (Doering)
Plate 18. fig. 4

Bulimus (Borus) d'orbignyi Doering, 1876:336.
S. (Borus) lutescens var. *d'orbignyi,* Pilsbry, 1926:6.
Helix (Cochlogena) nucleus d'Orbigny, 1835:14 [not *nucleus* Sowerby].
Bulimus nucleus, Darwin, 1840 (1):9.
Bulimus (Borus) nucleus, Strobel, 1874:20.
Bulimus (Borus) lutescens australis Martens, 1876:23.
Strophocheilus (Microborus) d'orbignyi, Bequaert, 1948:172, pl. 12, fig. 4; pl. 32, figs. 6, 7.
Strophocheilus (Austroborus) lutescens d'orbignyi, Parodiz 1949b:189-190.
Microborus lutescens dorbignyi, Hylton Scott, 1965:59-63.

The typical S. *lutescens* is found only in Uruguay. The perfectly allopatric and clearly distinct subspecies S. *lutescens dorbignyi* from the province of Buenos Aires has been clearly recognized since the time of d'Orbigny and Darwin. Fossil specimens, abundant in the Pleistocene, show that the differences between S. *lutescens lutescens* and S. *lutescens d'orbignyi* were less marked than in the living populations after allopatry was completed. The revised specimens are from the cliffs of the Quequén Salado River (about 120 km. west of Quequén Grande) 40 km. north of the Atlantic coast (near Irene) in Buenos Aires province, Chapadmalal formation, upper Pliocene. They were collected by Doello-Jurado in 1925. One specimen is complete and the other is in fragments embedded in the hard matrix of calcium carbonate and silica locally called *"tosca."*

Studying the anatomy of S. *lutescens dorbignyi,* Hylton Scott (1965) found differences of lung structure, tract of the genitalia, jaw, and pedal sole. Hylton Scott considered these differences sufficient to render *"Microborus" (Austroborus)* as a separate genus.

The type of S. *l. dorbignyi* was in the ANC when I observed it years ago, but in a recent visit to that institution it was not possible to locate the specimen.

Superfamily BULIMULACEA (Orthalicacea)
Family BULIMULIDAE (Orthalicidae)

According to H. B. Baker (1956, 69:133), Orthalicacea Albers & Martens, 1860, and Orthalicidae Tryon, 1860, should have priority over Bulimula- [cea-idae]. Bulimulinae, Odontostominae, and Orthalicinae were given family rank by Wenz (1938). A great number of subgenera and minor divisions have been proposed in recent years (more than 100 subgenera listed in Wenz), but many of them do not have clear definition and are based only on shell characters which overlap among groups, making the classification very difficult at the genus level. A good revision is necessary. In fossils most of the characters of the minor divisions are unobservable, and identification work allows only the use of broad, *sensu lato* genera.

The family is typically Neotropical, with the majority of the species in South America, *Rabdotus* in the southern United States, and *Naesiotus* in the Galapagos Islands. A few genera outside the Americas: *Placostylus* in New Zealand; *Aspatus* in the Solomon Islands; and *Prestonella* in South Africa, a *Bulimulus*-like representative of the Amphibulimidae [inae] which resembles *Eudioptus* by convergence.

The oldest fossils known are from southern Argentina in Patagonia, where the superfamily nowadays is very sparsely represented (*Peroneaus ameghinoi* Ihering at Bahia Sanguinetto on the coast of the Gulf of San Jorge in the southernmost limit of the living species) because of ecological conditions. Since the early Tertiary the Bulimulacea have had a great adaptive radiation on the continent and the living species number more than a thousand (see Note 43).

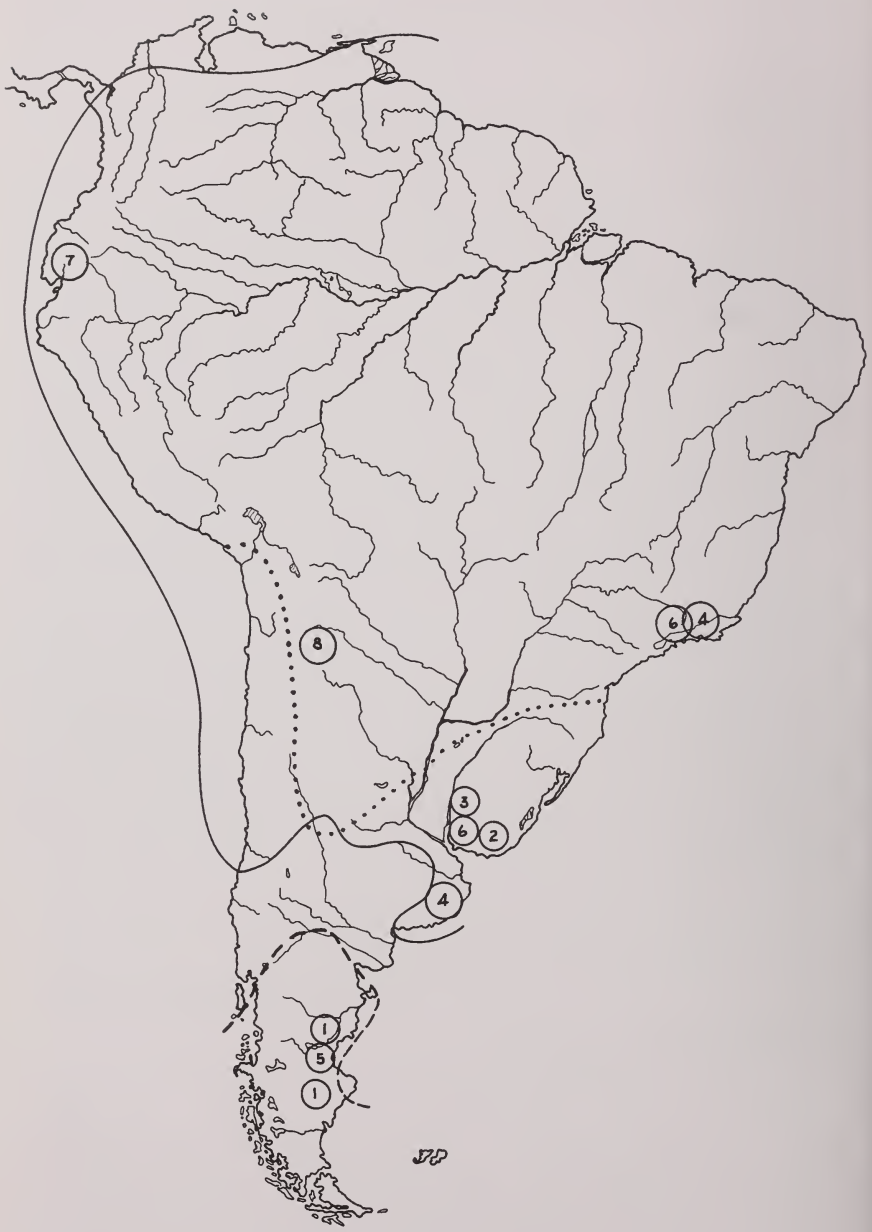
Subfamily BULIMULINAE
Genus *Thaumastus* Albers, 1860

Type: *Bulimus hartwegi* Pfeiffer

Generally "*Bulimus*" of authors.

Thaumastus patagonicus Parodiz
Plate 17, figs. 7, 8

ORIGINAL DESCRIPTION (translation): "Shell oval-elongated, with 5 whorls of which the last corresponds to 65% of the total length, compressed laterally and especially at the outer side of the aperture; the aperture is semioval below and occupies 42% of the total length, with the internal margin oblique and superiorly angulated. Diameter corresponding approximately to 38% of the length. In the


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holotype the apex is lacking, but in smaller paratypes the five whorls are complete. The sutural line compared with other fossil gastropods of same size (*Megalobulimus*) is more oblique (18°) and very deep in the cast, with vestiges of upper margination as it is a common feature in the living species of *Thaumastus*."

DIMENSIONS: L. 80 mm., major d. 31.5 mm., minor d. 30.5 mm.; last whorl 55 mm. ventral, 45 mm. dorsal; penultimate whorl 15.5 mm. x 23 mm.; aperture 34 mm. x 19 mm.

TYPE LOCALITY: Holotype and six paratypes (internal casts) from Cañadon Hondo on the Río Chico, Chubut, Argentina; Casamayor formation, Eocene. Collected by G. G. Simpson during the Scarritt Patagonian Expedition in 1931. Another, smaller, specimen, of which only the last two whorls of the cast are preserved, was collected by C. Burmeister in 1887 at "Rio Chubut." A label in F. Ameghino's handwriting says "*probable horizonte de Pyrotherium*" (which is Casamayor). This specimen is only 40 mm. long and its suture is deeper. Type in MACN.

With the exception of some living species also found in the Pleistocene (*Thaumastus magnificus* Grateloup), *T. patagonicus* is the oldest and only fossil species known in the genus. Living species are not found in Patagonia.

Genus *Paleobulimulus* Parodiz, 1949

Type: *P. eocenicus* Parodiz

Paleobulimulus eocenicus Parodiz

Parodiz, 1949c:177, figs. 1, 2.

ORIGINAL DESCRIPTION (translation): "The cast is of conic-oblong shape, with vestiges of having a small umbilical perforation. Five whorls (protoconch partially broken away), the last corresponding to about 80% of the total length, relatively convex, and rounded at the base; penultimate whorl a little less than 20% of the total length and about 1/5 of the last whorl. The major diameter is half of the height. The spire is short forming an angle of 34°. Suture slightly impressed, with vestiges of a slight internal margination between the two last whorls, and with an inclination of 10° in relation to the basal line. The columellar axis is 5° inclined to the left. Aperture oval, rounded at the base and narrow above, without columellar folding, but shows that it had had a peristome reflexed inferiorly; the upper angle of the aperture overlaps the middle line slightly. On the posterior side of the body whorl there are weak folds, impressed probably by other, stronger, lines of growth from the original inner side of the shell into the cast, but not constituing a regular striation."

MAP 6

——— Northern and southern continental distributional limits of living Strophocheilidae. 1-4. Fossil localities.

– – – – – Southern limit, living Bulimulidae. 5, 7. Fossil localities.

. Southern limit, *Epiphragmophora*. 8. Fossil locality.

1. Paleocene. 2. Oligocene. 3, 6. Miocene. 4, 7, 8. Pliocene. 5. Eocene.

DIMENSIONS: L. 25 mm., major d. 12.5 mm., minor d. 11 mm., last whorl 20 mm., penultimate 4 mm., aperture 13.5 mm. x 8 mm.

TYPE LOCALITY: From the region of Mallin Blanco, Chubut, Argentina, in strata which according to the geologist collector Dr. T. Suero, belong to the "*Capas con Astraponotus,*" that is, Musters formation, Eocene. The type in an internal cast. Type in MACN.

The differences between *Paleobulimulus* and the fossil *Thaumastus* of the same age are like those among the living species of *Thaumastus* and *Bulimulus*. The forms closer to *Paleobulimulus eocenicus* among the living species are those of the subgenus *Lissoacme*, as in *Peronaeus (L.) ameghinoi*. This is the oldest known *Bulimulus*-like form, greatly separated in time from the living species (Note 44).

Genus *Bulimulus* Leach, 1815

Type: *Bulimus guadalupensis* Bruguiere
= *B. exilis* Gmelin.

Bulimulus (sensu lato) fazendicus Maury

Maury, 1935:7, fig. 11.

ORIGINAL DESCRIPTION: "Shell small for the genus, conic-pyramidal, perforate, very neat and trim in appearance; remarkable for its many and very narrow whorls, the adult comprising nearly 9 volutions. The shell is widest near the base and tapers rapidly and evenly to the acute summit. The extreme apex formed by the earliest whorl appears, however, slightly obliquely flattened, due to its sudden increase in convexity. The earliest whorl seems entirely smooth, but one specimen shows on the third volution fine, nearly vertical striae. As a whole the shells are smooth except for microscopic, oblique wrinkles. Aperture ovate, lip thin, columella nearly straight. The most perfect shell measures in length 17 mm. of which 8 mm. are occupied by the spire and the remaining 9 mm. by the body whorl. Greatest width of the shell 10 mm. Length of aperture measured obliquely 6 mm., greatest width of aperture nearly 5 mm. Dr. Pilsbry examined this fossil and found it was not closely related to any living member of the genus. The larger number of whorls is its most prominent feature."

TYPE LOCALITY: Fazenda São Jose at Itaborai, Rio de Janeiro, Brazil, from same strata containing *Itaboraia,* Miocene, collected by A. Lamego. Type in AMNH.

The external features of the shell recall those of *Protoglyptus*, from which it differs in its smooth protoconch.

Genus *Itaboraia* Maury, 1935

Type: *Itaboraia lamegoi* Maury

The contour of the shell resembles that of *Neopetraeus*, but *Itaboraia* is characterized by a prominent fold on the columella, the expansion also covering the umbilical area. This genus is monotypic with:

Itaboraia lamegoi Maury
Plate 19, fig. 13

Maury, 1935:10, figs. 6, 7.

DESCRIPTION: Medium sized (32 mm. x 17 mm.), fusoid to bi-conic in shape and solid. Seven whorls rapidly tapering but the earliest whorl is not preserved; in the third whorl fine ribbing commences (about 35 oblique riblets of growth shown in oral face on the penultimate whorl, very regular). The rest of the shell sculptured with microscopic, cord-like riblets. The aperture is as high as the width of the shell, very angulated above and semiangulated below. Like the preceding species (*Bulimulus fazendicus*), the relationships and status of this genus are uncertain, but it resembles *Rhinus*.

TYPE LOCALITY: Same as *Bulimulus fazendicus*. Miocene. Type in AMNH.

Subfamily ODONTOSTOMINAE
Genus *Cyclodontina* Beck, 1837

Type: *Clausilia pupoides* Spix
= *Pupa inflata* Wagner

Subgenus *Plagiodontes* Doering, 1876

Type: *Helix dentata* Wood.

Cyclodontina (Plagiodontes) dentata (Wood)
Plate 19, figs. 4-7

Helix dentata Wood, 1828 (Index Testaceologicus Suppl.): pl. 8, fig. 71.
Cyclodontina (Plagiodontes) dentata, Parodiz, 1957:28.

This is the species which in its profuse synonymy was frequently referred to as *Helix sowerbyana, H. brasiliensis,* or *Pupa labyrinthus* (for complete synonymy and references see Parodiz 1939:715-716). It is the common, and best-known species of the genus formerly called "*Odontostomus*" of La Plata River region, north of Buenos Aires province and Entre Ríos in Argentina and southern Uruguay. It is found in Pleistocene deposits of the same area. I have not seen Tertiary specimens of this species but Caorsi & Goñi (1958:58) found it in the upper strata of the Fray Bentos limestone, near Mercedes, Uruguay, indicated as Miocene, associated with *Strophocheilus globosus*.

Subfamily ORTHALICINAE
Genus *Porphyrobaphe* Martens, *in* Albers, 1860

Type: *Bulimus iostoma* Sowerby

Porphyrobaphe iostoma bilabiata Pilsbry
Plate 19, fig. 8

Pilsbry & Olsson, 1941:13, pl. 8, fig. 9. Hoffstetter, 1948:32, 36.

This subspecies of the well-known type-species of *Porphyrobaphe* was indicated by its author for the Canoa formation, Pliocene, of western Ecuador. "The single example has a shorter spire than recent shells, but it has been somewhat 'telescoped,' the width of the antepenultimate whorl thereby much reduced. Otherwise it agrees well with the modern form. L 53.5 mm." (Pilsbry).

It is surprising to find this single, large land snail among the fossils of the Canoa formation, which otherwise is entirely marine (with 144 species, most of them newly described as extinct). Evidently it has drifted and been mixed with Canoa fauna. Its Pliocene age needs verification.

Porphyrobaphe iostoma iostoma is very common in the uppermost Pleistocene above the last marine terrace (Tablazo inferior, T3, after Hoffstetter) of the Santa Elena Peninsula, west of Guayaquil. The aeolic sandy sediments of the same terrace contain numerous fossil shells and fragments of *Porphyrobaphe*, which at present does not live in that area but somewhat to the north in more humid conditions.

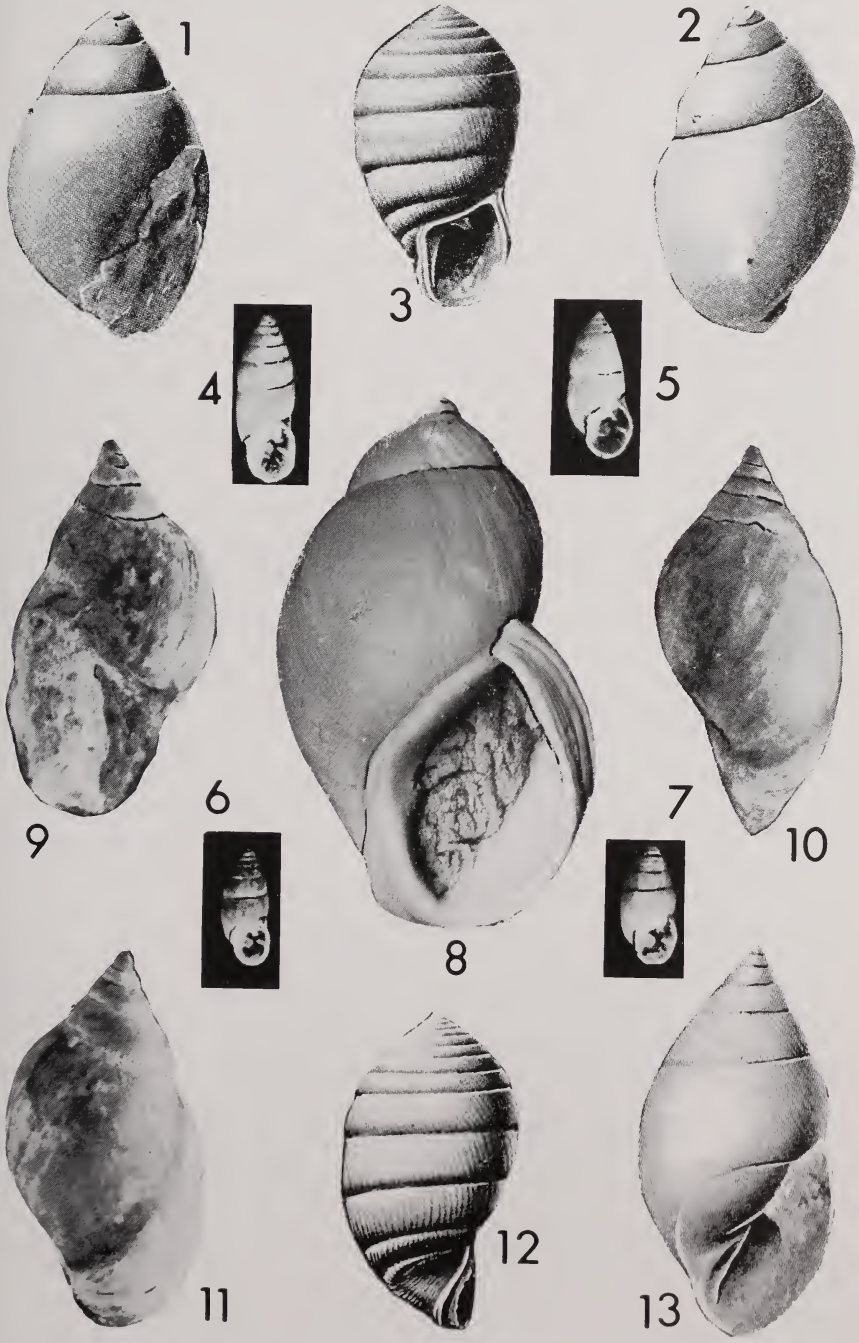
TYPE LOCALITY: Punta Blanca, W. of Guayaquil, Ecuador. Type in ANSP.

Superfamily STREPTAXEA
Family STREPTAXIDAE (*ex* Artemonidae)
Subfamily ENNEINAE (Ptychotremalinae-Streptostelidae)

The Streptaxidae are represented in South America mainly by the subfamily Streptaxinae with six genera *(Martinella, Scolodonta, Artemon, Streptaxis, Streptartemon, Saicostoma).* Members of the subfamily

PLATE 19

1,2. *Strophocheilus sanctijosephi* Maury. Type, x1.
3,12. *Brasilennea arethusae* Maury. Type, x1½.
4-7. *Cyclodontina (Plagiodontes) dentatus* (Wood). x1.
8. *Porphyrobaphe iostoma bilabiata* Pilsbry. Type, x1.
9-11. *Physa wichmanni* Parodiz. Type, x2.
13. *Itaboraia lamegoi* Maury. Type, x1½.


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Enneinae are practically absent in the Recent fauna, and known only by the fossil name *Brasilennea*.

Genus *Brasilennea* Maury, 1935
Brasilennea arethusae Maury
Plate 19. figs. 3, 12

Maury, 1935:4, figs. 1-5 (monotype). Zilch (Wenz, 1960. 578, fig. 2025).

ORIGINAL DESCRIPTION: "Shell of medium size, the adult form convexly subcylindrical with the greatest breadth near or a little above the center. Volutions many, with their sides convexly flattened. Sutures linear and distinct. Apex obtusely pointed, but only very slightly elevated. The first two-and-a-half to three whorls are smooth, glossy, with their sides gently convex. Thereafter the subsequent whorls become more and more strongly sculptured with very fine, narrow, closely set, sharply defined ribs, which on the center of the shell number nearly three to a space of one millimeter. There is a graceful change in the direction of the trend of the ribbing, the ribs on the spire being very oblique, but those on the last volution are almost vertical. In the adult shell the last whorl narrows markedly, and on the aboral side shows two strong external sulci, one central, the other basal and defining the conspicuous perforation of the shell. Aperture with two pronounced folds within. One fold is on the columella, well shown on one specimen to be strong and rounded, while the other is sharper and is on the upper inner margin of the aperture, nearly median. Outer lip straight, with a parallel lamella on a perfect shell. Height of the adult 25 mm., greatest width 14 mm., height of the aperture measured obliquely 9 mm., greatest width 7 mm."

TYPE LOCALITY: Fazenda São Jose, Itaborai, Rio de Janeiro, Brazil, from upper Miocene strata (Itaboraia limestone II), found with *Itaboraia* and *Bulimulus*. Type in AMNH.

According to Pilsbry, who examined the specimens, *Brasilennea* is totally new for America. It closely resembles *Ptychoon,* a subgenus of *Ptychotrema* of Recent tropical Africa, but differs in the larger number of whorls and the presence of a parietal lamella.

Superfamily HELICACEA
Family XANTHONYCIDAE (Helminthoglyptidae)
Subfamily EPIPHRAGMOPHORINAE

According to H. B. Baker (1956) Xanthonycidae Strebel & Pfeffer, 1879, antecedes Helmintoglyptidae Pilsbry, 1939.

Genus *Epiphragmophora* Doering, 1875

Type: *Epiphragmophora hieronymi* Doering

Epiphragmophora is an aberrant genus in the family, characterized

by its very short spermathecal duct, and Pilsbry considered it as a subfamily by itself. But shell features are almost indistinguishable from those of other Xanthonycidae, especially of the Soronellinae from California — a case of strong parallelism. In fact the type of *Sonorella*, S. *hachitana* Dall, from Mexico, was described originally as *Epiphragmophora*. Following in similarities are the Helminthoglyptinae, which are known in western North America from the Cretaceous. The living species of *Epiphragmophora* are found in abundant populations in central and northwest Argentina, extending to Bolivia and Peru, but are absent in the eastern regions of the continent. Some subgenera have been recognized in the northern area of their range. The only fossil species known, here described, is *Epiphragmophora, sensu lato*. The subfamily seem to be a late Tertiary northern immigrant.

Epiphragmophora feruglioi, new species
Plate 18, figs. 5, 6

DESCRIPTION: Shell of small size, very flat, carinated at the periphery of last whorl, forming a sharp angle which divides the ambitus of the body whorls into two zones in which the upper surface is flatter. Four-and-a-half whorls (peristomatic area broken in the holotype), rapidly increasing after the first two. Umbilical area with wide perforation. The fossil cast does not show any particular sculpture. Suture well impressed. The aperture appears expanded to the right, causing the columellar axis to appear to be strongly inclined in the opposite direction.

Holotype measurements: Height 5 mm., major d. 17 mm., minor d. 13.5 mm. In other specimens of same proportions the spire is a little more elevated but not acute, and the upper surface of the last whorl above the carina a little more convex.

In size this species approaches *E. puella* Hylton Scott from Catamarca, but the outline of the shell is closer to *E. villavilensis* Parodiz, also living in Catamarca. This new form, however, is more angulate-carinated and flatter than any other known living species.

TYPE LOCALITY: Right margin of Itiyuro River, between Campo Durán and Angostura, N.E. of province of Salta, Argentina, near the Bolivian border. Collected by E. Feruglio in 1930 from the red clays (rather chocolate in color) of the "Subandean Tertiary," upper Pliocene (Note 22). When given to me for identification, I suggested to Dr. Feruglio that it was very probably a new form, different from the living species, and as such was indicated by Feruglio and by Frenguelli (1937:475). On account of the mammal fauna contained in the same strata at Campo Durán, these authors, as well as the paleontologist A. Cabrera, concluded that the formation corresponds to the Araucanian age in the uppermost Pliocene, comparable to sediments of Chapadmalal in the S.E., and probably transitional with Uquian. Type in CM.

Discussion and Conclusions

The non-marine mollusks of the South American Tertiary are represented by 22 families: four of bivalves, eight of prosobranch gastropods, and 10 of pulmonate gastropods. Of the species, about 37 per cent are Paleocene, about 13 per cent Eocene, about 14 per cent Oligocene, about 24 per cent Miocene, and about 19 per cent Pliocene (some of the species are common to more than one epoch). Several species (corresponding to 5 per cent of the total) survived up to the Recent epoch: *Diplodon chilensis* from the Oligocene; *Diplodon guaranianus, Strophocheilus globosus* and *S. haemastomus*, and *Cyclodontina dentata* from the Miocene; and *Porphyrobaphe iostoma* and *Strophocheilus lutescens* from the Pliocene. Two families became extinct in South America after the Paleocene: Viviparidae and Valvatidae.

The Paleocene and Eocene fresh-water shells from different localities are of the same genera, and sometimes the same species. The conditions of deposition of these fossils were very similar in all Paleocene locations: mouths of fresh-water bodies, estuaries, or strands of bay-like environments, and they are often found mixed with brackish-water, or even marine species. The unstableness of coastlines was a peculiar feature of the Paleocene, intensified on the western side of South America as a consequence of the tectonic disturbances during early Andean orogeny. Land gastropods are mainly Eocene and belong to genera still living or to closely related ones; usually they were found in strata composed of tuff, with a large proportion of volcanic ash.

According to their known or probable origin, families can be divided into three groups. The first group, and most numerous in genera and species, is that of northern (Nearctic) origin, which migrated to South America at the close of the Cretaceous, or just about at the threshold of the Danian epoch: the Hyriidae, Viviparidae, Valvatidae, Pleuroceridae, Thiaridae, and Potamididae. Fossils of these families are not found in the South American continental area before the Paleocene, and they form the group that Pilsbry termed "Cenogeic," to which must be added other families of a later migration from North America and Central America during the end of the Miocene and during the Pliocene: the Ampullariidae, Aperostomidae, Streptaxidae, and Xanthonycidae (and Clausiliidae?). The early, Senonian-Danian migration, was only one way, from north to south. But the later movement was

a two-way migration; some southern families, like Bulimulidae, extended north and even reached Kansas and Illinois in Recent times, and others from Central America descended toward the tropics. The fauna of the later Tertiary migration never reached the austral regions in Patagonia, as those of the early Tertiary did.

The second group is composed of those families autochthonous to South America: Chilinidae, Strophocheilidae and Bulimulidae. Chilinidae are endemic to the southern region and part of the eastern region. Strophocheilidae were introduced into Trinidad and Barbados in Recent times. Bulimulidae expanded more into Central America and the southern United States, and according to Pilsbry, *Bulimulus dealbatus* now inhabits Illinois. Its expansion seems to be very recent, although Dall had mentioned another genus (*Anctus*?) of the Bulimulidae for the Miocene of Florida. These three families correspond to what Pilsbry called the "Eogeic" or the "Archhelenic" group.

As in all other continents, there has existed in South America a number of fresh-water families, of very old, world-wide distribution since very ancient times, which do not offer clues to their original centers of dispersion. This is the third group, which is formed mainly by the Sphaeriidae, Hydrobiidae, Lymnaeidae, Planorbiidae, Physidae, and Ancylidae. In the Hydrobiidae, *Potamolithus* is an endemic genus with restricted distribution parallel to that of *Neocorbicula* in the eastern section of the continent. *Littoridina*, abundant in the Pleistocene and Recent, is surprisingly sparse in the Tertiary. *Lyrodes, Tropidebora, Liris, Toxosoma,* and *Dyris* seem to have had a later expansion from the northwestern section of Peru and Ecuador northward, and are related to a relict fauna recently discovered in northern Mexico (Coahuila).

African relationships of certain families, indicated by some authors, especially Ihering, are dubious and can be assumed only for the Mycetopodidae (Mutelacea) and perhaps the Corbiculidae, but in this family, the genus *Polymesoda* and its Tertiary relative *Sogamosa* are

MAP 7

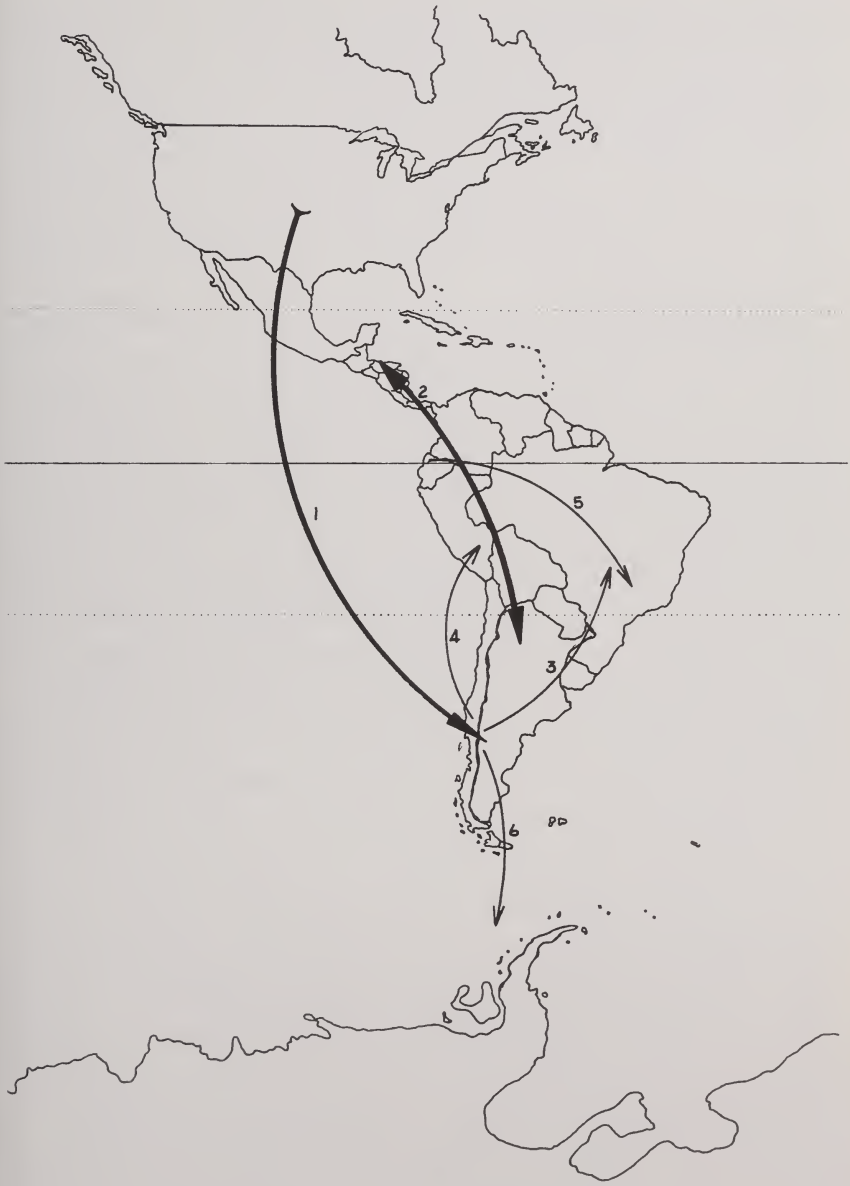
Main migrations (heavy lines):

1. One-way migration during late Cretaceous-Paleocene (mollusks and early mammals).
2. Two-way migration in late Miocene-Pliocene.

Secondary dispersions (thin lines):

3-5. Secondary dispersion in middle Tertiary.

6. Probable dispersion through Antarctica during Tertiary.


1
2
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6

more likely of North American origin. *Neocorbicula,* even if close to the Old World *Corbicula,* was already represented in South America in the earliest Tertiary and probably also in the Cretaceous, in a region that is positively not part of that area called Gondwana. The old genus *Eriphyla* is tentatively placed in the Corbiculidae, although its proper systematic position is still unsettled. The adaptive radiation of these two families must have been a very old one. The Strophocheilidae are not directly related to the African Acavidae as supposed; the two are anatomically distinct, and shell similarities of *Strophocheilus* and *Burtoa* are only convergent.

Fossil, naiad-like shells (*Naiadites, Paleomutela, Paleoanodonta,* and others) are abundant in the late Paleozoic and early Mesozoic of South America, and are referred to as "gondwanic" elements. But these are not related to any of the Tertiary or Recent fauna of Naiades. They probably represent a very primitive group of fresh-water mussels that became extinct before the Cretaceous. The most persistent genus of the true Unionacea, with the oldest fossil record, is *Diplodon* (Hyriidae), known by many species from the Triassic of Pennsylvania (Newark Series) and Texas. This genus became extinct in North America, but, appearing in the Paleocene of South America, continued up to the Recent with many species. As in other old groups of very early evolution, *Diplodon* changed very little during the Tertiary, but populations within species vary greatly because of their plasticity in adapting to different environments. In the cold region of Tierra del Fuego the genus did not survive, but it was living there in the Oligocene when the climate was more benign. Other genera of Hyriidae, *Triplodon* for example, evolved late in the Pliocene of northern regions.

The Mutelacea are found, fossil or living, only in warmer zones. Only one species, *Anodontites patagonica* (Lamarck), lives as far south as 40° latitude. The fossil record is scarce; earlier references to the African genus *Pleiodon* in the Cretaceous of Brazil proved to be *Paxyodon* (Unionacea). Some genera of Mycetopodidae are endemic to South America: *Monocondylaea* since the Oligocene, *Fossula* since the Miocene, and *Leila* since the Pliocene. The dispersion of *Monocondylaea* followed that of *Diplodon* from northwest to southeast. As for the genus *Mycetopoda,* Pilsbry (1921:36) described a species, *M. diluculi,* from the Triassic of Pennsylvania, found in the same strata with *Diplodon*: "while the generic reference is not positive, its characters, so far as they are legible, agree well with *Mycetopoda* [or a genus] closely similar." If this generic assignment of *M. diluculi* is con-

firmed, then the assumed origin of the Mycetopodidae as belonging to the Gondwanic-area concept is questionable.

The Viviparidae, abundant in the Cretaceous and the Recent of North America, were short-lived in South America after migration, and no species are known younger than Paleocene. They were accompanied in migration by *Pyrgulifera,* also extinct.

The Pleuroceridae were common during the Patagonian and Chilean Paleocene, judging by the large populations of the extinct *Paleoanculosa.* In northwestern and northeastern South America the fossil species belong to the living genera *Pachychilus* and *Doryssa.* The Thiaridae are represented by several genera now extinct: *Pyrgulifera* in the Paleocene (also known from the Cretaceous of Wyoming) and *Morgania* and *Hannatoma* in the Eocene and Oligocene of Peru, respectively. But more abundant in fossil and living species is the genus *Aylacostoma* (including *Hemisinus, Verena,* and *Longiverena*) found from Colombia to northern Argentina. The abundance of these fossil "melanias" is correlative with the ecological conditions that prevailed on the west coast of South America during the early Tertiary. The oldest Potamididae are found in the Paleocene of Bolivia and Argentina, and show a progressive northward dispersion, toward Peru in the Eocene and toward Venezuela in the Miocene.

Although paleontology (of continental mollusks, as well as mammals and other vertebrates) heavily supports the hypothesis of a late-Cretaceous-early-Tertiary land connection between North and South America, the actual area or migrational route has not been geologically established. From the known facts, however, it might be assumed that it took place through zones now submerged, along, and somewhat west of, the present Pacific coast; and that the introduction of the Nearctic elements took place first in the southern region, Chile and Patagonia, which at that time (the end of the Cretaceous) still was disconnected from the northeastern territory usually identified as the remnant of Gondwana. Extending from the Chilean coast below Concepción, there was in Paleocene times a long peninsula projecting northwest as far as San Felix and Juan Fernandez islands. Between that peninsula and the mainland the sea entered a narrow gulf. The peninsula probably looked like the present Baja California, but inverted and somewhat larger. Its disappearance was dated by Groeber (1963) in the Oligocene. The strand of the austral mass of land (equivalent to Ihering's Archiplata) can be traced by the brackish- and fresh-water strata stretching from Peru and western Bolivia to northern Argentina and

Patagonia, and it is likely that the Puca and San Jorge seas were at certain periods connected, although these seas may not have been synchronous in their beginnings. Within this order of ideas, Groeber (1939b:73) thought of his Río Grande formation, which is an anachronous complex of strata ranging from below the Danian to the Eocene. The union of the two land masses, old "Brasilia" with Archiplata, took place under rapidly and repeatedly changeable conditions, and the zone between the Colorado and Negro rivers shows in its geological structure the "scar" of such union. The Danian transgressions covered the great depression still in existence, entering from both Pacific and Atlantic sides. In the northwest, Ecuador, Colombia, and Venezuela, the effects of an earlier and vast Cretaceous transgression (where previously there was a three-branched Andean geosyncline, according to Schuchert, 1935), resulted in longer unstable periods. All these changes were correlative with the beginning and subsequent stages of the Andean orogeny.

When in 1911 Pilsbry published his report of the Princeton Expedition to Patagonia (1896-1899), it was surprising to find, under the title of "Non-Marine Mollusca of Patagonia," a discussion devoted mostly to faunas of the Parana-Uruguay basin and southern Brazil. But Pilsbry's real intention was to establish the continuity in time, of a fauna that had its origin in, or dispersed from, the south. Very few fossils were known at that time, but basing his observations on the Recent forms, Pilsbry pointed in the right direction. He divided the faunistic elements into three groups:

1. The oldest group of the southern hemisphere, correlative with the concept of Gondwana, or "Eogeic" fauna; 2. the middle-aged group that migrated from North America (which suddenly appears in the South American Paleocene, although Pilsbry knew no fossils) — the "Cenogeic" group; 3. the group of families of very early evolution, world-wide distribution, and uncertain origin. Such an approach agrees with our present conclusions based on the 22 families from which fossils have been found.

The first important discovery on these lines, in 1922, was that of *Viviparus*, from the Paleocene of Patagonia (at that time still considered Cretaceous), but the evidence of a massive faunal migration from the north was clarified by G. G. Simpson, in the 1930's, studying the early mammals of the Río Chico formation. The molluscan expansion from the south to the rest of the continent was in two main directions: one branch went northward along the western area and left abundant

fossils in the Oligocene and Miocene of Ecuador and Colombia, and from there turned south again in an easterly direction. The other advanced to the northeast, in Uruguay and southern Brazil, where speciation became intensive, but because of subsidence, erosion, refilling with modern sediments, and changes in the distribution of the continental waters, fossils from the intermediate zone west of the Paraná fault are rare. The Paraná fault was one of great magnitude (it must have been formed during the Pleistocene because deposits of this age are found at its upper and lower margins), and the Entre Ríos formation, which is found up to more than a hundred feet high on the cliff east of the Paraná in Entre Ríos, was found only by drilling several hundred feet down on the west side of the river (Santa Fe).

The earlier connection between North and South America was short-lived, and by the end of the Paleocene was already interrupted. The southern continent, now consolidated and again isolated, was the asylum in which the earlier immigrant Mollusca radiated into their present peculiar diversities. At the same time a bizarre fauna of mammals was evolving in isolation. The re-establishment of the land connection in the Pliocene, or perhaps late Miocene, thus made possible an exchange of faunas between North and South America that apparently continues in Recent times.

APPENDIX I

THE FRESH-WATER BIVALVES OF "UNIONID" TYPE FROM MISSISSIPPIAN TO TRIASSIC OF SOUTH AMERICA

From the late Paleozoic and early Mesozoic of South America a number of species of "Naiads" have been described or indicated:

Naiadites sp. Harrington	Barreal, San Juan, Argentina. Mississippian.
Naiadites sp. Frenguelli	Bolivia, Taiguati formation. Pennsylvanian.
Naiadites liagracielae Leanza	Rincon Blanco, Río Penas, La Rioja, Argentina. Pennsylvanian.
Carbonicola promissa Frenguelli	"Estratos de Tupe", San Juan, Argentina. Mississippian.
Carbonicola timenda Leanza	Rio Blanco, La Rioja, Argentina. Pennsylvanian.
Carbonicola mitis Leanza	Rio Blanco, La Rioja, Argentina. Pennsylvanian.

Carbonicola erratica Leanza	Rio Blanco, La Rioja, Argentina. Pennsylvanian.
Anthracomya diluta Leanza	Rio Blanco, La Rioja, Argentina. Pennsylvanian.
Paleomutela glabra Frenguelli	"Estratos de Los Rastros," La Rioja, Argentina. Pennsylvanian.
Paleomutela occidentalis Freguelli	"Estratos de Los Rastros," La Rioja, Argentina. Pennsylvanian.
Uniona ichigualasti Frenguelli	"Estratos de Los Rastros," La Rioja, Argentina. Pennsylvanian.
Uniona riojana Frenguelli	"Estratos de Los Rastros," La Rioja, Argentina. Pennsylvanian.
Paleoanodonta ramaccioni Frenguelli	Paganzo II, Argentina. Triassic.
Kidokia picardi Frenguelli	"Estratos de Los Rastros," La Rioja, Argentina. Pennsylvanian.
Terraia altissima Cox	Strada-Nova beds, Uruguay. Permian-Triassic.

With the exception of *Naiadites,* of which Pilsbry described species from the Triassic of York County, Pennsylvania, the genera have not been indicated for North America. *Carbonicola* and *Anthracomya* are known from Africa (Tanganyika), *Paleoanodonta* from Eurasia and Africa, and *Uniona* from Japan. The Carboniferous-Permian-Triassic species from South America have been referred to as "gondwanic," but as most of the genera also existed elsewhere during the late Paleozoic and early Mesozoic times (or earlier), Leanza suggested that the earlier "Gondwana" (or pre-Gondwana area) might have had some connections across the Tethys sea that separated the northern and southern lands. Frenguelli, however (1954:430), remarked that the so-called "northern forms" of the lower Gondwana flora, which sometimes were identified with similar species of the European Carboniferous, proved, after a more careful study, to be of different and peculiar southern types, although he thought they might be local survivors of a cosmopolitan pre-gondwanic realm of life. Nevertheless, the Tertiary-Recent Naiad fauna of South America does not seem to be related to those older types, but belongs instead to a stock that evolved in North America. In the case of the Mutelacea some ancient relationship with an African-Gondwanic stock may be likely, but there is no positive evidence that the Recent types derived from those older genera mentioned. Probably the Carboniferous-Permian-Triassic Naiad fauna represented a branch divergent from a primitive "Unionid-type," which became extinct before the Tertiary.

APPENDIX II

THE FOSSILS OF THE *FORMACION PETROLIFERA* OR "SALTA SYSTEM" DESCRIBED BY BONARELLI

In 1921 G. Bonarelli classified a large number of fossil gastropods from the Argentina-Bolivia border, giving provisional names, without description, to the graphic representation of the materials. A year later these fossils were taken to Europe by Doello-Jurado, who gave them to Cossmann for observation. Cossmann corrected some of Bonarelli's names and ratified others, but the comparisons were made with Paleozoic-Mesozoic gastropods from Europe. Not entirely satisfied with Cossmann's taxonomy, Bonarelli produced a more complete paper in 1927, distinguishing "forms" and "varieties" of forms, not species; in fact that author declared (1927:52) that he "does not see how it is possible to know what a species might have been in remote times" because there were not enough materials (most of his forms were based on small fragments). Furthermore, he clearly stated that he was able only to distinguish or "to fix with distinct names the slight differences among the fossils even if these actually were merely individuals of the same species." With this peculiar procedure, Bonarelli classified that fauna into 14 genera or subgenera (some new) and 77 forms, with specific nomenclature. With the exception of two, all his forms were new, assigned to a Triassic age, and in addition, indicated as marine.

But Bonarelli — who in those days belonged to the Argentine Bureau of Mines and Geology — returned to Europe in 1924 leaving his manuscript unfinished. It was concluded by P. Groeber "according to the opinions expressed verbally by Bonarelli in several occasions" and, although concurring with those opinions in the text, Groeber added a chapter with his own conclusions, assuming that the fossils were of Rhetic or even Bajocian age. In 1939, however, Groeber changed his views regarding the classification of the fossils and their age. He concluded that the gastropods were not Loxonematidae as Bonarelli thought, but brackish- or fresh-water "melanids," and that the age of the *Calcareo Dolomítico (=Formación Petrolifera)* could not be older than Tertiary or the latest Cretaceous. Before entering into further discussion of that fauna, it is pertinent to give a complete list of Bonarelli's "forms" here (the family and genera are listed according to Wenz):

Family LOXONEMATIDAE
Subfamily ZYGOPLEURINAE

Genus *Zygopleura* Koken, 1892

Z. *turgida* Bonarelli	Carbajal
Z. *turgida eliator*, Bonarelli	
Z. *turgida proversicosta* Bonarelli	
Z. *paucinodosa* Bonarelli	
Z. *spinocosta* Bonarelli	
Z. *cossmanni* Bonarelli	
Z. *argentina* Bonarelli	
Z. *insignis* Bonarelli	
Z. *decarlessi* Bonarelli	
Z. sp.	
Z. *crassinodis* Bonarelli	Maimará
Z. *scopesi* Bonarelli	
Z. *multicosta* Bonarelli	
Z. *gallardoi* Bonarelli	
Z. *pustulosa* Bonarelli	
Z. *maimarensis* Bonarelli	

Subgenus *Katosira* Koken, 1892

Z. *(K.) zygopleuroides* Bonarelli	Carbajal
Z. *(K.) zygloleuroides elatior* Bonarelli	
Z. *(K.) zyglopleuroides intermedia* Bonarelli	
Z. *(K.) communis* Bonarelli	
Z. *(K.) pseudovetusta* Bonarelli	
Z. *(K.) recticosta* Bonarelli	
Z. *(K.) carbajalensis* Bonarelli	
Z. *(K.) carbajalensis baculoides* Bonarelli	
Z. *(K.) carbajalensis ornatissima* Bonarelli	
Z. *(K.) carbajalensis alta* Bonarelli	
Z. *(K.) carbajalensis angulicosta* Bonarelli	
Z. *(K.) ?dubia* Bonarelli	
Z. *(K.) rapidecrescens* Bonarelli	
Z. *(K.) clathrata* Bonarelli	
Z. *(K.) conoidea* Bonarelli	
Z. *(K.) brachyspira* Bonarelli	
Z. *(K.) obliquicosta* Bonarelli	
Z. *(K.) longobardi* Bonarelli	Maimará
Z. *(K.) percrassa* Bonarelli	
Z. *(K.) groeberi* Bonarelli	
Z. *(K.) nagerai* Bonarelli	

Subgenus *Kittliconcha* Bonarelli, 1927	
Z. (K.) doelloi Bonarelli	Carbajal
Subgenus *Anoptychia* Koken, 1892	
Anoptychia sp.	Carbajal
Genus *Hypsipleura* Koken, 1892	
H. ? binotata Bonarelli *H. ? brackebuschi* Bonarelli	Carbajal
Genus *Tyrsoecus* Kittl, 1892	
T. andinus Bonarelli *T. moniliformis* Bonarelli *T. perarmatus* Bonarelli	Carbajal
Subgenus *Stephanocosmia* Cossmann, 1895	
T. (S.) disputabilis Bonarelli *T. (S.) frequens* Bonarelli *T. (S.) microcantha* Bonarelli *T. (S.) tyrsoecina* Bonarelli	Carbajal
Subgenus *Goniospira* Cossmann, 1895	
T. (G.) ameghinorum Bonarelli	Maimará

Family SPIROSTYLIDAE

Genus *Doellocosmia* Bonarelli, 1927	
D. doelloi Bonarelli	Carbajal
Genus *Spirostylus* Kittl, 1894	
S. elegans Bonarelli	Tres Cruces
Subgenus *Heligmostylus* Cossmann	
S. (H.) bonarellii Cossmann	Tres Cruces

Family PURPURINIDAE

Genus *Gonioconcha* Bonarelli, 1921	
G. striata Bonarelli *G. striato-spinata* Bonarelli *G. spinata* Bonarelli *G. spinata brachyspira* Bonarelli *G. nodosa* Bonarelli *G. nodosa evolutior* Bonarelli	Tres Cruces

Family PROCERITHIIDAE
Subfamily PROCERITHIINAE

Genus *Procerithium* Cossmann, 1902

Subgenus *Eocerithium* Bonarelli, 1927

P. (E.) potosensis (d'Orbigny)	Maimará

Subfamily METACERITHIINAE

Genus *Protofusus* Bonarelli, 1927

P. carbajalensis Bonarelli	Carbajal
P. saltensis Bonarelli	
P. andinus Bonarelli	
P. convexigyrus Bonarelli	

Subfamily PARACERITHIINAE

Genus *Paracerithium* Cossmann, 1902

Subgenus *Brachycerithium* Bonarelli, 1921

P. (B.) seminudum Bonarelli	Tres Cruces
P. (B.) microstoma Bonarelli	
P. (B.) intermedium Bonarelli	
P. (B.) evolutum Bonarelli	
P. (B.) major Bonarelli	
P. (B.) lacrymigerum Bonarelli	
P. (B.) helicoidale Bonarelli	
P. (B.) ornatissimum Bonarelli	
P. (B.) dupliciornatum Bonarelli	
P. (B.) pauciornatum Bonarelli	
P. (B.) recticosta Bonarelli	
P. (B.) minus Bonarelli	
P. (B.) feruglioi Bonarelli	

The Loxonematidae *(sensu lato)* were formerly included within the Pyramidellidae, and Fischer placed the older genus *Loxonema*, and *Paramelania*, in the Pseudomelaniidae, indicating that the family was entirely composed of marine fossils. The numerous genera of Loxonematidae range in time from late Paleozoic to early or middle Mesozoic, and are not known in the Tertiary.

Otto Haas in 1953 still supported Bonarelli's views of a Triassic age for the fossils of Carbajal and Tres Cruces. It is not our concern here to discuss the fauna studied by Haas from Cerro Pasco in Peru, which according to that author may be Triassic and marine. What should be

clarified is that the Cerro Pasco specimens have nothing in common with the fossils of the *Calcareo-Dolomítico*, and the correlations derived are unsound.

Groeber indicated, as early as 1939, that shell characters for the "melanids" and loxonematids given by Koken are very confusing, since generic descriptions by Koken were exactly the same for both groups, word for word. Another circumstance mentioned by Groeber is that the fauna of Carbajal, Tres Cruces, and Maimará is composed exclusively of gastropods, a case that rarely occurs in marine sediments, in which the bivalves are always more abundant. For Groeber all the fossils were "melanians," and this "opens the way to consider those strata as Cretaceous and fresh-water" (in other places Groeber says Danian, that is, Paleocene). When Fritzsche (1924) described the fossils of the Puca formation of Bolivia and northwestern Argentina, he also indicated a Cretaceous age (for the marine ones), and as we know now, the uppermost strata of Puca (fresh-water) belong to the lower Tertiary (see Notes 2 and 3).

The author who, after Bonarelli, investigated and compared the fossil record and stratigraphy in that area was Frenguelli (1937). He concluded that all the mollusks of the "Calcareo-Dolomítico" are in continental deposits, forming numerous populations in thin strata, mostly of lacustrine origin, and that a marine phase appears only northward (the specimens studied by Fritzsche) in Bolivia. Frenguelli also had the opportunity to examine most of Bonarelli's "forms," in collections from Cerro Colorado, Salta, at the geological museum of the Y. P. F. (Argentine Oil Bureau), and he declared that it is impossible to separate them into species, even of a single genus, and that in his opinion all could be reduced to two or three species of "Melaniidae" with very variable ornamentation.

Added to the observations by Groeber and Frenguelli are the geological studies of Schlagintweit (1941) and Ahlfeld (1946); the faunula described by Pilsbry (1939) from El Molino, Bolivia; the vertebrates described by Cattoi & Freiberg (1958 — see Note 28); the recent stratigraphic studies by Ruiz Huidobro (1961 — see Note 55); and finally the relationship of certain genera and species of the *Calcareo-Dolimítico* = *Formación Petrolifera* = "Salta System" with others from the Paleocene of Patagonia. All these data indicate an early Tertiary age for the fauna in question. Taking into consideration Bonarelli's own uncertainty about the taxonomy at the species level, this fauna can be reduced to the following, relatively identifiable taxa:

SPECIES	LOCALITY	GENUS IN BONARELLI
1 — *Pyrgulifera feruglioi* (Bonarelli)	Tilcara	*Brachycerithium*
Aylacostoma (Hemisinus) ? *majus* (Bonarelli)	Tilcara	*Brachycerithium*
Aylacostoma (Verena) striata (Bonarelli)	Tres Cruces	*Gonioconcha*
Aylacostoma (Verena) brackebuschi (Bonarelli)	Carbajal	*Hypsipleura*
2 — *Dorysa maimarensis* (Bonarelli)	Maimará	*Zygopleura*
3 — *Potamides decarlesi* (Bonarelli)	Carbajal	*Zygopleura*
Potamides doelloi (Bonarelli)	Carbajal	*Kittliconcha*
Potamides turgida (Bonarelli)	Carbajal	*Zygopleura*
Potamides potosensis (d'Orbigny)	Maimará	*Eocerithium*

1 = Thiaridae; 2 = Pleuroceridae; 3 = Potamididae.

All these species are discussed in the taxonomic part of this work, with the exception of *Aylacostoma (Hemisinus) majus*, the systematic position of which is doubtful. The latter is different from the other species of *"Brachycerithium"* (= *Pyrgulifera*). Wenz (1961:732) included it as a subgenus of *Paracerithium*.

Notes

1. According to von Huene and Oliveira & Leonardos, the Palmitas sandstone in Uruguay probably corresponds to the Bauru formation. The age of the lower section, after Kraglievich and Doello-Jurado (personal communication), must be Senonian, but the upper, as it appears at Serra de Botacatu *(Arenito Bauru)*, is probably Paleocene and is distinguishable from the *conglomerato basal* (Oliveira & Leonardos 1943: 605).

2. As the name Puca was applied indiscriminately to both marine and fresh-water sediments, the proper term for the upper continental series along the Puca strand is Miraflores, since the typical fauna of this locality in Bolivia is fresh-water.

3. In some places the Puca lies on Paleozoic rocks and in others fills eroded Cretaceous surfaces. The base of the Puca complex (Pirgua formation) is Cretaceous. Correlations with late Gondwana, which have been suggested, are very unlikely. All Gondwana sediments were carried from the east.

4. Groeber (1939b) included the fresh-water Lonquimay, the marine San Jorge, the *piso Ranquil*, and other strata ranging from Senonian to lowest Eocene, in a complex that he called "Río Grande formation." In one of his last papers (1963) he correlated the Chilean fresh-water Paleocene with the upper portion of Roca (Roca II), but persisted in calling the typical Rocanean Roca "I." Apart from these chronological inconsistencies, Groeber clearly stated (1963:140) that, east of the Bío-Bío the Lonquimay strata are Paleocene, overlaid by his *Chilelitense Superior* as "paleocene-infraeocene." The lowest Eocene bears *Diplodon transandinus*. Roca "I" is not Rocan (Danian) in the true sense, but corresponds to what Feruglio (1949) and Casamiquela (1964) identified with the *Capas de Ortiz* (Mastrichtian), known in the Limay River valley, and coeval with Lefipan and Cazadoran. It should be noted that, even if the fresh-water fossils of the Paleocene of Patagonia and Chile belong to the same formational unit, the marine beds of both sides of the Andes do not. Their respective areas of invasion did not make contact, which explains the possibility of finding similar continental species mixed with dissimilar marine species in areas that correspond to opposite strands. On the other hand, Bruggen,

Guiñazu, and Groeber agree in considering Concepción at its base as synchronous with "Notostylops" (Casamayor).

5. Sanjorgian is distinguished from the marine Senonian in the same area by the disappearance of such Cretaceous genera as *Trigonia, Alectryonia*, and *Inoceramus*, as well as of ammonites. Apparently only two species of oysters survived from the late Cretaceous to the Tertiary: *Ostrea rionegrensis* Ihering and *O. clarae* Ihering. There are many species common to the Rocan and Salamancan:

Ostrea neuquena Ihering
Ostrea ameghinoi Ihering
Myochalmys salamanca Ihering
Gryphaea rostrigera Ihering
Exogyra callophyla Ihering
Venericardia paleopatagonica Ihering
Meretrix chalcedonica Ihering
Aporrhais chubutensis Ihering
Nautilus valenciennesi Hupe

6. Feruglio (1938) and Groeber (1939b) indicated that the Roca is represented by two levels separated by regressive periods, but actually Roca "I" equals the *Lahillia luisa beds*" (Cazadoran; see also Note 4). And comparing Feruglio's later observations, the "old" Roca seems to be synchronous with Ortiz and Lefipan. In the Senonian there are different facies (whether they represent short time units has not been clearly established yet) of large marine transgressions, the Cazadoran, Bustamante, Lefipan, Ortiz, Malargue, and Huantrico. In the Danian, there were also marine transgressions, the Roca at Río Negro and the Salamanca at Chubut, with brackish-water intercalations where they contact Jahuel.

7. The name *Ostrea guaranitica* Ihering, 1899, from Park-Aik on the Sehuen River, added some confusion because this species belongs neither to the "*Formación Guaranitica*" in the sense that Ameghino and Ihering used the term, nor to the Guaraní region of northern Argentina and Paraguay. Ihering also referred (1899:64) to another single valve from Arroyo San Juan near Santa Ana on the Upper Paraná, which, he said, "I judge to be identical with the previous one." But years later (1907b:50,52) he recanted: "as it is incomplete and badly preserved, it is not possible to identify its geological age." The first illustration of *O. guaranitica* appeared in Ameghino, 1906:55, fig. 7.

8. At first (1918) Windhausen included the "Sehuenense" in the Sanjorgian, later (1924) reclassified it in a lower, a brackish-water facies of the *Lahillia luisa* beds, and finally (1925) placed it as an "austral facies of the Salamanca-Danian Sea."

9. Berry indicated two different ages, first Miocene and then Cretaceous, for the same flora. The first plants were collected by C. W. Washburn, of the commission headed by Bailly Willis, in 1912-1913. Years later Berry received new materials from Piatznitzky, but was not informed that both collections came from the same strata and locality. In 1925, Feruglio, Frenguelli, and Piatznitzky made joint observations on both sides of the Chalia (Sehuen) River at Mata Amarilla. The report, published by Feruglio (1937), did not mention either the flora or the fresh-water fauna, and still placed the Sehuenan as marine in the upper Cretaceous. This lapsus was clarified by Frenguelli (1953b; see also Note 15).

10. Since Frenguelli (1930a) defined "Sehuen" as coastal-fluvial-palustrine, the presence of abundant flora, unless the mixture is strictly peripheral, gives Sehuen its own stratigraphic unity, for which that author subsequently proposed the term "Chalian."

11. The expansion of the fresh-water fauna may be correlative with that of the flora from the Cretaceous-Tertiary boundary into mid-Tertiary. Frenguelli recognized two epochs: an older, subtropical in character, and a younger, related to the strata of Seymour Island in northwestern Antarctica. It has been often suggested that continental mollusks migrated, as the Hyriidae did, from Patagonia to Australia during Tertiary times.

12. The "Banco Verde" (below Banco Negro) is divided into a lower section (= early Salamanca) and an upper section, "C," of Simpson (1935b). Because of its microfossils, Frenguelli considered section "C" marine. The "Banco Verde" is glauconitic, while Banco Negro is bentonitic with *Diplodon* and *Ostrea* mixed. This seems to agree with Simpson (1937:4): "The 'banco negro' is commonly taken by convention as the base of the supra-Salamanca series . . . It may be the base of the Río Chico or . . . an intercalated series between Salamanca and Río Chico of distinct age or facies. The banco seems to be conformable (or only locally disconformable) with Salamanca."

13. These turtles belong to the genera *Najadochelis* and *Gyremia,* known from the Cretaceous of North America.

14. Feruglio (1938:332-333) gives the following sequence for the complex (for him Senonian-Danian) on both sides of the Sehuen River: (1) a facies of shallow sea; (2) oscillating regressive phase with estuarine sediments; (3) very short transgressive phase with exclusive marine fauna; (4) regression of long duration which established the continental regime in the entire area. The transgressive phase (3) is chronologically placed in the latest Senonian or in the Danian, "contemporary with, or of little difference in age from, the transgression of Roca-Salamanca in Chubut." The Sehuenan represents the strand between (3) and (4).

15. In his posthumous work, Feruglio (1949-1950) still placed the Sehuenan in the Senonian of Mata Amarilla. Simpson's first interpretation (1933:3) correlated Sehuen, in Frenguelli's terms, with Río Chico, although in subsequent works Simpson entertained doubts about the Sehuenan in the southern locality: "probably not synchronous with all central Patagonia Sehuenense of Frenguelli." But Simpson's first statement was confirmed by new explorations by Frenguelli (1953b): "If Piatnitzky and Feruglio confirm, as Ihering did, that the Sehuenan is contemporary with Salamanca-Rocanean, it is not possible to maintain an upper Cretaceous age for sediments comparable to those in the Paleocene."

16. Compressed casts of *Diplodon* were found by Casamiquela (1964:292) in the "Senonian lacustre" at the edge of Caru-Lafken (Green Lake) overlying the "Pehuenche" and underlying Casamayor "characteristic of the lower section of Jahuel strata at Roca." The same author indicated that Jahuel-Roca are not always mixed: at Jacobacci, Río Negro, there is only Jahuel, and at Coli Toro only marine, strata.

17. In spite of Simpson's clarifications, on several occasions, of the Pehuenche, other geologists continued using that term for younger strata. Feruglio (1949:197), while concurring with Simpson, persisted in using the name Pehuenche for Danian-Montian beds, evidently recognizing "the impossibility of breaking the habit" wrongly established by oil geologists. In 1941 Simpson wrote, "The general adoption of an error (even when it is general) is not a very sound argument for its perpetuation after its falsity has been exposed." In addition, it should be noted that the term Pehuenche does not conform to present standards of stratigraphic nomenclature, because it was not based on a typical toponym and has only ethnological connotations. The only

available name for that series of the so-called "strata with dinosaurs" is Neuquenean, given by Frenguelli (1930a). This name also includes part of Keidel's "Huincul Group" and the lower portion of the "Portezuelo Group." But later Groeber called "Neuqueniano" a melange of lower Senonian, Chubutian, strata containing *Lahillia luisa* fossils (marine), and Roca-Salamanca; at its base Groeber places the "Ranquil sandstone" as Neocomian, *without fossils.* But in previous works he said this formation contained *Viviparus, Melania, Diplodon,* and *Ceratodes,* and assigned them en masse to the Albian.

18. The name "Palmirense" (Kraglievich, 1931), apparently has priority and was recognized by Simpson (1940) for Uruguay. But the name Palmiran was used for the Colombian Senonian, and here Lambert's "Fray Bentos" is adopted to avoid confusion.

19. Gabb said (1869) that the fossils indicated a "marine or perhaps brackish-water fauna." Conrad (1874a), who studied the fossils from Orton's second trip to Pebas, confirmed it. If the Pebas formation in Peru is Pliocene, it must be not much lower than the boundary with the Pleistocene strata, and many of its species survived into the Quaternary of Brazil, wrongly indicated as Pliocene before Simpson's correction of 1961.

20. Ameghino's "Laziarense" is probably Chapadmalan-Uquian in age (Pliocene, after Simpson, 1940). Kraglievich, Bordas, Frenguelli and others agreed with the concept of a vast Arauco-Entrerian unit from middle Miocene (Paranean) to lower Pliocene (Chapadmalan). It is interesting to note that Ameghino (1906:244) had already treated the Auracanian and the Entrerrian in a comprehensive way, and Simpson (1940:690) recognized a stratigraphic group of Arauco-Entrerrian strata, from Chasicó below to Chapadmalan above, divided into geographical subgroups, Araucanian, Entrerrian, Eopampean, and Rionegran.

21. The Calchaquean corresponds to the lower level of the Araucanian complex, according to Frenguelli (1937), and Riggs & Patterson (1939). The Calchaquean is mid-Miocene, while the typical Araucanian is Pliocene. In Mendoza the Calchaquean appears west of San Rafael, along the Diamante River and Cachueta, where, Groeber said, there were gypsum beds containing *"Corbicula stelzneri."* All authors who have referred to the *Estratos Calchaquies* reported seeing that species of *Corbicula, in situ,* but specimens in collections are very rare

and it is not certain that all authors referred to the same thing (see also page 93). Frenguelli also called these strata "Santamarian."

Like *Corbicula stelzneri*, *Azara occidentalis* Doering is another *nomen nudum*. Together with these forms, Frenguelli also found *Littoridina* in the Salta zone of the Valley of Santa Maria, which corresponds to the *Hydrobia*, *Littorinella*, *Bythinia*, and *Paludestrina* mentioned by several authors since Bondenbender (1924). The latter considered the Calchaquean to be upper Cretaceous or lower Tertiary, but his stratigraphy was very confusing and he probably confounded Calchaquean with Puca. A complete discussion of the subject, not pertinent here, may be found in the exhaustive work of Frenguelli (1936).

22. Cabrera and other authors considered the "Subandean Tertiary" (= Steinmann's Jujuy-Schichten) no older than late Pliocene or early Pleistocene.

23. The *Diplodon* species from the Triassic of Pennsylvania were described by Pilsbry (1921,1927), with some addenda by Richards (1944,1948). All are from the Newark series of York County shales along Little Conewago Creek (near York) and at Mont Clare (near Phoenixville). The species are:

Diplodon pennsylvanicus Pilsbry
Diplodon borealis Pilsbry
Diplodon wanneri Pilsbry
Diplodon carolusimpsoni Pilsbry
Diplodon yorkensis Pilsbry
Diplodon lewisi Richards
?*Mycetopoda diluculi* Pilsbry
Naiadites triassicus Pilsbry
Naiadites wanneri Pilsbry

The best preserved of these species is *Diplodon pennsylvanicus*, known from the two mentioned localities, and showing the unmistakeable characters of *Diplodon*.

Other Triassic *Diplodon*-like forms, are these "*Unio*" species:

TEXAS

Unio subplanatus Simpson
Unio dumblei Simpson
Unio granulatus Simpson
Unio dockumensis Simpson

MASSACHUSETTS (Connecticut River valley)
Unio emersoni Troxell
Unio willrahamensis Emerson

24. Ihering first identified *Diplodon colhuapiensis* as *D. diluvii,* probably because, as he declared several times in his letters to Ameghino (official edition of Ameghino's complete works), d'Orbigny's volumes on the paleontology of the "Voyage" were not available to him at the time he received specimens from Roth, Hauthal, and the Ameghino brothers.

25. At Colloncurá River, in Neuquén, there are strata of different ages bearing specimens of *Diplodon.* The "Capas con *Notophagus*" (with *D. patagonicus*) are separated from the Colloncurean above (with *D. rothi*) by strong disconformity. Groeber gave a new name, "Palaocolitense," to the tuff of Colloncurá, with chronological equivalence to the Burdigalian (Miocene). For Simpson (1940:666) the question whether Colloncurá is a distinct stage between Santacruzian and Friasean could not be answered until its fauna was better known (see also Bordas 1939b).

26. Marshall's assumption that *Prodiplodon* is ancestral to *Diplodon* is unsound. *Diplodon* is known from the Triassic of North America, while the species indicated as belonging to *Prodiplodon* are from the upper Pliocene.

27. An example is the case of the large and characteristic land snail *Strophocheilus oblongus haemastomus,* in sediments that drifted and mixed with marine fossils in the sands of the Entre Ríos cliffs.

28. Turtles of the genus *Podocnemis* are known from the Cretaceous of Arkansas (*P. barberi* Schmidt) and Alabama (*P. alabamensis* Zeugel). In South America, *P. harrisi* Pacheco and *P. argentinensis* Cattoi & Freiberg are known from Jujuy, northern Argentina. Both have been indicated as upper Cretaceous, but the Jujuy species belong to the "Margas Multicolores" (Santa Barbara formation), which is equivalent to Miraflores in Bolivia and evidently of late Pucan age (see also Note 2).

29. *Monocondylaea franciscana* Moricand is apparently conspecific with *M. lentiformis* Lea. The size of both forms is about the same, but *M. lentiformis* is more solid and inflated, and less winged, with the posterior margin more angulated (but less than in *M. paraguay-*

ana). The umbo is nearer the anterior end (in *M. franciscana* it is weak and flat), and the single tooth larger and stronger. The prismatic zone of *M. franciscana* is wider, and the color darker. Southern specimens of *M. lentiformis* (Paso de los Libres, Corrientes, Argentina) are relatively larger, but in other characters are identical with those from northern populations, and according to Bonetto (1966), both *M. franciscana* and *M. lentiformis* are synonyms of *M. corrientesensis* d'Orbigny, 1835. Their areas overlap in the zone of the Uruguay River between Corrientes and Río Grande do Sul. The typical form of *M. franciscana,* however, is rather constant in the north. *M. felipponei* Marshall is the same as *M. lentiformis*, according to Haas.

30. F. Haas (1931:96) included *Anodontites sirionos* in the synonymy of *A. patagonica* Lamarck. The two species are undoubtedly related and the range of *A. sirionos*, according to d'Orbigny is N.W.-S.E., from the mountain streams of Bolivia, to Uruguay. The true *A. sirionos* is probably restricted to Bolivia, being the same as the form briefly described by Doello-Jurado (1924:239) as *Anodontites lizeri* from the Mocoví and Ivarí rivers (the illustration of *A. lizeri* was published separately in "Memorias" of the Argentine Museum in 1924).

31. Marshall (1925) indicated differences, probably of taxonomic value, in the micro- and macro-sculpture of the periostracum of *Anodontites*. Although such differences are recognized, they have specific value only and, according to Bonetto (1965), coincide with the generic uniformity in *Anodontites.*

32. The typical *Anodontites patagonicus* Lamarck corresponds to the form described by d'Orbigny as *A. puelchana* from San Javier, Río Negro. It is an isolated form and very rare, which is to be expected for a species extra-limital to the genus range. C. T. Simpson included *A. puelchana* in the synonymy of *A. limnoica* d'Orbigny, with an unusually large and very unlikely range from Patagonia to the Amazon River. *A. patagonicus* differs from *A. latomarginata* Lea (= *A. uruguayensis* Lea), which also was included as a synonym. D'Orbigny did not mention *A. patagonicus* for comparison when describing *A. puelchana*, and only two authors have mentioned *A. puelchana* as such: Doering (1881) and Pilsbry (1911).

Ortmann, however, received some specimens of the typical *A. patagonicus* — which I observed — from the Limay River in Neuquén, which he (1921) identified with *A. puelchana.* These specimens are thin,

fragile, greenish, and elongated, and agree with the original illustrations of Lamarck's *Anodonta patagonica* and *A. puelchana*. They are substantially different from *A. latomarginata*, which is thick, solid, usually larger and more rounded, and has a dark reddish-brown periostracum.

Unio membranacea Hanley, which also was usually placed as a synonym of *A. patagonicus* (= *Unio matoniana* d'Orbigny), is in my opinion an immature and badly preserved valve of *Diplodon variabilis*.

33. For "*Melania tuberculata*" Wagner (not Müller, 1776), Ihering (1909:322) proposed the new name [*Hemisinus*] *spica*.

34. The strata from Casamayor (Eocene) to Deseado (Oligocene) were called "Deseadiano" by Frenguelli (1930a). Kraglievich (1930) used "Colhuehuapiense" for the base of Casamayor, while the true Colhuehuapian, which is Oligocene, was named "Trelewense." Groeber (1939b) still referred to the same strata as "tuff with mammals." To avoid renewed confusion about these and other Groeber references, it must be noted that his paper of 1939b was outdated (the MS was completed years before the publications of Schlagintweit, Frenguelli, Feruglio, and G. G. Simpson). With the exception of "Rocanense," Groeber gave new names to most of the old known strata, and his "Río Grande formation" included marine, fresh-water, and terrestrial sediments of different ages. (See Not 4).

35. Until 1906, Ameghino included in the *Formación Guaranitica* all the Patagonian sediments from the Pehuenche to what is now known as the Deseado formation. D'Orbigny, in 1842, gave the name *Tertiaire Guaranien* to reddish beds of northeast Argentina along the Paraná River, older than the *Tertiaire Patagonien*. It was Doering who thought that the red sandstones of the Río Negro, bearing dinosaurs, belonged to the same extensive formation. In this he was followed by Ameghino. The term "Guaranitica" is now restricted to the old, Cretaceous, strata of Corrientes, Misiones, and Paraguay, and totally excluded from the Patagonian stratigraphy.

36. Wilckens's (1906) opinion that the Sehuenan was purely a facies of the *Lahillia luisa* beds (Cazadoran) proved to be wrong. The characteristic marine fauna containing the large Cardiidae bivalve *L. luisa* Wilckens is found in the Monte Cazador series of the upper Turbio River, southwest Santa Cruz, near the Chilean border (northeast of Puerto Natales).

37. Although *Diplodon chilensis* and *D. transandinus* are apparently in the same group as *D. granosus* and *D. granosus multistriatus*, these two pairs differ greatly in distribution. Recently (Parodiz, 1968: 14,18) I indicated that "*Unio granosus*" was originally described from "rivers of the Guiana" which run independently to the sea, isolated from the Amazon and other Brazilian river systems by the high Sierra of Tumucumaque. All other localities afterwards referred to for *D. granosus* are from river systems 1500 miles to the south, and it is very unlikely that such identifications are correct. On this account, *D. granosus* stands as a poorly known and isolated species, and is different from the so-called *D. granosus multistriatus* (the latter form = *D. ellipticus*), of the San Francisco River basin.

38. The *Diplodon guaranianus* group is a complex corresponding to what at present is termed a "superspecies" (a group of very closely related, monophyletic species — which also has been called *Artenkreis*, after Rensch). It is generally equivalent to what in taxonomic practice has been often indicated as a "species group," but the concept is purely biological and phylogenetic, independent of the rules of taxonomic nomenclature.

39. Designation of subspecies encounters certain resistance among paleontologists. It is true that the term "subspecies" applies properly to populations that are synchronous and allopatric, while in a fossil population the term also has a dimension of time. Outstanding authorities, however, like G. G. Simpson, recommend the use of subspecific categories. The basis for this view is that recognition of small successional species would be unacceptable, but that temporal subspecific divisions are acceptable with larger successional species. Still, there is a difference between this kind of subspecies and the purely geographically isolated subspecies in neontology.

40. While *Diplodon wymani* still stands as a subspecies of *D. delodontus*, *D. uruguayensis* does not (see Parodiz, 1968:11). These closely related species and subspecies commonly hybridize — as they do with *D. expansus* — and their offspring are mistakenly classed as "races." *D. diluvii* is probably an ancestral or ancient form of that superspecific complex.

41. From Las Lajas, near the bend of the Agrio River, in Neuquén, Burckhardt (1903) reported *Eriphylla argentina*, which he had previously (1900:23,pl.24,figs.3–7) assigned to *E.* aff. *E. transversa* of the

European Neocomian. In shape, sculpture, hinge, and pallial sinus, this species of *Eriphylla* is very much like one of the *Neocorbicula*, and it may be included in the Corbiculidae rather than in any other family. But it represents an old stock of giant shells (length 60 mm.), and perhaps still has a brackish-marine habitat. This species may be younger than Neocomian, but is still Cretaceous. Stoliczca (1871) advanced an opinion that many fossil shells described as *Astarte* should be transferred to *Eriphylla*.

42. Article 26(a) of the I.C.Z.N. rules that names based on a compound are to be united without a hyphen, and treated as though they had been originally published in that form.

43. Bulimulidae were common in the Pleistocene of South America. Most species are still living:

Spixia charpentieri (Grateloup)	Buenos Aires formation at Miramar.
Spixia tucumanensis (Parodiz)	Buenos Aires formation at Paraná.
Spixia spixi (d'Orbigny)	Buenos Aires formation at Paraná.
Spixia martensis (Doering)	Buenos Aires formation and Arazati at Uruguay.
Plagiodontes patagonicus (d'Orbigny)	Post-Pampean, at Bahia Blanca.
Plagiodontes daedaleus (Deshayes)	Post-Pampean, at Dulce River, Santiago del Estero.
Plagiodontes dentatus (Wood)	Post-Pampean, at Punta Chaparro, Uruguay.

44. *"Bulimulus" ameghinoi* Ihering was described from a single fossil specimen from the Buenos Aires formation at the Chapadmalal River. Later, it was found living as a fairly common form in eastern Patagonia as far south as Bahia Sanguinetto in Santa Cruz (Parodiz, 1944), the southernmost locality registered for living Bulimulidae in South America. I have seen other specimens from many other localities in Buenos Aires province. Ihering also mentioned *Bulimulus gorritiensis* Pilsbry (a species living in the vicinity of Maldonado, Uruguay) as fossil in the Pleistocene of Chapadmalal. But in the numerous post-Tertiary collections I revised, I never found this species, and the fossils mentioned are probably small individuals of *B. sporadicus* (d'Orbigny).

45. Feruglio (1950,2:230-231) coordinated the previous stratigraphic studies of the Arauco region in the following systems:

1. "Piso" Concepción	PALEOCENE
a. Boca-Lebu, marine	
b. "Capas de Millongue"	EOCENE
Lower, continental (=Lonquimay), with "mantos de carbón."	
Upper, marine.	
Unconformity	
2. "Piso" Navidad	LOWER OLIGOCENE
Lower, similar to "Juliense" in Patagonia.	
Upper, marine.	
Unconformity	
3. "Capas de Tubul", marine.	UPPER OLIGOCENE

46. Mammals related generically to those of the Santa Cruz formation (e.g., *Propachyrucos*) appear as the oldest in the Oligocene of Uruguay. In the Miocene of Colombia (Honda formation), Stehlin (1939) recognized *Scleromys*, a genus of the Santa Cruz beds. Douglas (1914) reported *Nesodon*, another Santacruzan genus, from the middle Tertiary of the Maury River in Bolivia. And according to Simpson and Patterson, the *Griphodon* discovered by Anthony from the Huallaga River, middle Tertiary of Peru, is related to the pyrotheres (Deseado formation, lower Oligocene) of Patagonia.

47. The type locality of Chichinales is near that of the Roca, and the Chichinales sediments fill the eroded surfaces of that marine stage, as described by Wichmann (1927). But previously, Windhausen (1918) had found in these strata the remains of *Colpodon* (identified by C. Ameghino), and because of the age of those strata thought Chichinales could be synchronized with the Colhuehuapian.

48. *Lithococcus*, or a very closely related genus, lives also in northern Mexico (relict fauna of Cuatro Ciénagas, Coahuila). In fact the new genus and species recently described as *Mexithauma quadripaludium* Taylor (1966: 204, pl.19, figs. 58–63) bears great similarity to *Lithococcus* from Ecuador.

49. The subfamily Littoridininae, proposed as new by Taylor (1966) had been previously recognized by other authors (see Wenz, 1960). It was used by Gray in 1857 as a family name.

50. *Doryssa andicola* and *D. maimarensis* somewhat resemble the genus *Abyssochrysos* Tomlin, 1927 (family Abyssochrydae, after Wenz, related to the Thiaridae). But this is a recent genus from South Africa and the case is one of simple convergence, as in *Melanoides*. Although

those two species of *Doryssa* may be the basis for a new subgenus, it is more convenient to keep them in *Doryssa, sensu lato*, until the systematics of this difficult group of "melanias" is clarified.

51. Bonarelli placed *Gonioconcha* in the family "Purpurinidae," also suggesting relationships with *Murex fusiformis* from the Jurassic limestone of Württemberg, Germany!

52. In the geological literature of Patagonia, especially in Feruglio's works, a species is frequently referred to as *Actaeonella patagonica*, from the beds containing *Potamides patagonensis* (Sehuenan). The identity of such a species was never verified. Feruglio sometimes gives authorship to Ferussac, and others attribute it to Ihering. If the authors meant *Actaeon patagonicus* Ihering (1907b:117, pl.4, fig. 1), which is from the lower Miocene, then it is evidently not an *Actaeonella*, which belongs to another subfamily. The shape approaches that of *Actaeon* (*Fictoacteon*) from the Cretaceous of Texas, but the spire is longer and is gradate, a feature that does not occur in the Actaeonellidae. As it is a brackish-water form, it may be one of the Chilinidae. Another specimen of *Actaeon* described by Ihering in 1907 as *A. argentinus* has all the characteristics of the genus *Tornatellaea*.

53. I have seen living specimens of *S. oblongus haemastomus* from southern Brazil attaining a length of 107 mm., with a folded lip 14 mm. wide. I have also seen a similar one from Barbados. In other features they looked like the typical *S. oblongus*. Many individuals of *S. oblongus elongatus* Bequaert from Uruguay have a folded lip as wide as in *S. oblongus haemastomus*.

54. This allopatry, as well as the speciation of forms that formerly were widely distributed between southwestern Buenos Aires province and Uruguay, was completed during the Belgranean transgression of the middle Pleistocene, when a vast area around Bahia Blanca, the austral sierras, and all the present Atlantic coast were covered by the sea. Only the high lands of the sierras were above water, preserving a land fauna which today is a relict, and with species that no longer live in the surrounding pampas. That fauna, however, lived, before the transgression, in the entire area which today is La Plata River, and the coastline extended without interruption from Mar del Plata to Punta del Este or beyond. The low plains along the coast then contained numerous lacustrine bodies of water, and the topographical situation must have been similar to that now prevailing along the

coast of Río Grande do Sul in Brazil. La Plata River is a very young basin, which came into existence during the early Holocene, after the great fault of the Paraná was formed (see pages 34, 195).

55. Ruiz Huidobro (1961) established the following stratigraphic series for the late Mesozoic and lower Tertiary of northwestern Argentina:

PALEOCENE	Río Sali formation	Subandean Tertiary, Santa María Valley ?
	Santa Barbara formation	"Margas Multicolores" ?
CRETACEOUS	"Calcareo-Dolomitico"	Sandstones and limestones with gastropods.
	Pirgua formation	

56. These also include *Diplodon minor*(Roxo) = *Ecuadorea minor*, from the Jurua River beds in Amazonas, which, as well as those of the Acre River, are Pleistocene.

57. From the Triassic of Brazil a species was described as "*Diplodon*" *lucianoi* Maury. This form does not bear any similarity to *Diplodon* or any other known South American fresh-water mussel. It probably belongs to a marine shell.

58. The name *Chubutolithes* was given by Ihering (1922, no title; note on "*Chubutolithes*" and "*Rocalithes*." Palaeont. Zeitschr., 4:113) to problematic, non-marine fossils from the early Tertiary of Patagonia, These fossils were considered by different authors as a kind of invertebrate (Bordas, Feruglio, Frenguelli, Schiller) or as coprolites (Windhausen). My first observation of the fossil led me to think also of the eggs of some large land gastropod. Simpson (1935c: 13, 22) found *Chubutolithes* in the Chubut Valley near Gaimán Nuevo, adding that it "occurs definitely in the Casamayor [formation, Eocene] farther south." That author also gave a general description of the fossils. The specimens I have observed were collected by Wichmann in 1926 at Nahuel Niyeu, Río Negro, some 200 miles northwest of those of Simpson, together with bones of fishes (*Ceratodus*?), remains of turtles and characteristic fresh-water mollusks, all Jahuelan.

Dr. Craig Black of the Carnegie Museum collected fossils from Eocene strata of Wyoming that are similar to *Chubutolithes*. R. W. Brown (1934, 1935, Jour. Washington Acad. Sc., 24:532; and 25:256) described fossil larval chambers of mining bees, *Celliforma spirifer*,

also from the Eocene of Wyoming, and H. A. Tourletot (1957, Smithsonian Misc. Coll., 134(4):1-27) found similar fossils in the Wind River Basin. It is evident that these North American and Patagonian fossils are the same kind of larval chambers, although *Chubutolithes* and *Celliforma* may not be the same generically. Frenguelli (1938, Physis, 12:349, fig. 3) also referred to nests of wasps, and balls of beetles from the Casamayor formation of Santa Cruz, comparable to those of living scarabeids of the genus *Megathopa;* but the shape is always globular or pyriform, instead of almost cylindrical as in *Chubutolithes.* It is interesting to note that fossil nests of wasps appear also in the limestone of Miguez (Oligocene), Uruguay, together with *Strophocheilus charruanus.*

Chubutolithes seems to have been common in the early Tertiary of Patagonia, since authors of most geological and paleontological works referred to it. The strata in which it is found forms a "horizon" by itself, of yellowish tuff, on the top of Casamayor formation and below the eroded surface later filled with the base of the marine Patagonian.

59. After this MS was concluded, the author received a paper by M. Klappenbach & J. Olazarri, "Notas sobre Strophocheilidae" (1966), in which a statement about the status of *Strophocheilus charruanus* had been made, agreeing with our own conclusions except for the reference to *S. sanctijosephi* as a synonym.

Sumario

Las especies conocidas de moluscos continentales del Terciario en Sud América, corresponden a 22 families y 48 géneros. De las especies, aqui discutidas, el 37 por ciento son del Paleoceno, 13 por ciento del Eoceno, 14 por ciento Oligoceno, 24 por ciento Mioceno and 19 por ciento Plioceno; estos porcentajes incluyen especies que aparecen en más de una formación o época. Aunque la fauna reciente de los moluscos no marinos es muy afin a la del Terciario, el número de las que han sobrevivido sin modificación substancial es reducido, correspondiendo solo al 5 por ciento. La sobreviviente más antigua es del Oligoceno, *Diplodon chilensis*; otras seis son del Mioceno-Plioceno: *Diplodon guaranianus, Strophocheilus globosus, haemastomus y lutescens, Cyclodontina dentata, Porphyrobaphe iostoma.*

En el Paleoceno unas pocas familias se extinguieron en Sud América, (Viviparidae, Valvatidae), asi como algunos géneros de Pleuroceridae, Thiaridae y Corbiculidae, pero casi todos los otros grupos, especialmente los Hyriidae experimentaron una radiación adaptiva intensiva, hacia las formas modernas. Por otra parte aquellos que habian alcanzado un alto grado de evolución en tiempos muy antiguos, se modificaron poco como grupos de especies, pero muestran actualmente una extrema variabilidad individual y de población por adaptación a diferentes medios, sin consecuencia genetica.

Los taxa nuevos, descriptos o denominados en este trabajo son en su mayoria del Paleoceno: *Eriphyla miraflorensis, Lioplacodes feruglioi* y *bolivianus, Paleoanculosa* (Nuevo género) *patagonica, Pyrgulifera sehuena* y *Potamides chaliana; Taphius waltheri* y *Lymnaea klappenbachi* del Oligoceno; *Neocorbicula stelzneri* Mioceno y *Epiphragmophora feruglioi* Plioceno.

La posición estratigráfica, o edad, de muchas especies, ha sido corregida, puesta al dia o correlacionada. Muchas de las formas del Paleoceno habian sido descriptas como cretácicas, (y hasta triásicas) desde que en la columna estratigráfica de los primeros autores la posición del Daniano era todavia discutida. Los fósiles del Paleoceno y Eoceno de diferentes y distantes localidades, son todos de géneros, y muchas especies similares, y las condiciones bajo las cuales vivieron eran también muy iguales: estuarios y desembocaduras de corrientes de agua dulce, o bahias y caletas en costas bajas e inestables, donde

las especies fluviales muchas veces aparecen mezcladas con las salobres o marinas. La inestabilidad de las costas era un fenómeno general en el Paleoceno de Sud América, y especialmente en en el área pacífica y extremo sur, correlativo probablemente con los movimientos de la primera fase de la orogenesis andina. La correlación de los estratos marinos con los continentales, es de gran ayuda para la determinación de la edad relativa de los últimos.

La fauna conocida del Paleoceno, parece haber tenido en su mayoría su origen en Norte América. Muchas especies fósiles pertenecen a géneros que se conocen del Cretaceo de Wyoming y hasta del Triasico de Pennsylvania. Una migración con dirección única hacia el sur, ocurrió inmediatamente después de la primera comunicación establecida entre ambas Américas, al final del Cretaceo. Tal migración de moluscos continentales es correlativa con la de los mamiferos primitivos que aparecieron por primera vez en Sud América en la formación de Río Chico del Paleoceno. Las localidades y expansión registrada de los primeros moluscos continentales del Terciario, parecen indicar que la ruta migratoria hacia el sur ocurrió a lo largo, y posiblemente más hacia el oeste, de la actual costa pacífica de Sud América.

Una segunda migración, operando en ambas direcciones con cambio mutuo de taxa entre Sud y Central-Norte América, tuvo lugar durante el Mioceno superior y Plioceno inferior. Nuevas familias entraron en la región Neotropical entonces en formacíon: Ampullariidae, Aperostomidae, Streptaxidae, Xanthonycidae. También típicas familias sudamericanas como Bulimulidae, se extendieron hacia el norte tanto como hasta Illinois en Estados Unidos. El conocimiento de la dispersión de las faunas pleistocenicas y vivientes, señala que estos movimientos migratorios continuan al presente.

Un corto número de familias, como Strophocheilidae, Chilinidae y Bulimulidae, son autoctonas de Sud América, con sus fósiles más antiguos conocidos del Paleoceno. El género *Epiphragmophora*, endemico en la fauna reciente y de gran diversidad específica, pertenece a una familia (Xanthonycidae) de origen norteamericano, con su aparición en Sud América en el Plioceno. Otros géneros endemicos, como *Neocorbicula* y *Potamolithus* corresponden a familias cuya distribución pasada y presente es universal.

Del Paleozoico superior — Mesozoico inferior se conocen un buen número de géneros de almejas de tipo nayade *(Carbonicola, Uniona, Kidokia, Terraia,* y *Naiadites)* encontradas en localidades de Sud América que se atribuyen al área de Gondwana. Pero estas no muestran

ninguna relación con las almejas de agua dulce de las faunas terciaria y actual, y son grupos extinguidos. No existe evidencia positiva de que alguno de los moluscos continentales terciario-recientes, tenga relación con la fauna africana, y los casos que encontramos invocados en la temprana literatura son simple ejemplos de convergencia *(Strophocheilus-Burtoa)* o ya de errónea identificación como el *"Pleiodon" priscus* mencionado para el Cretaceo de Brasil, que ha resultado ser un Hyriidae del Paleoceno.

Algunas familias como Lymnaeidae, Planorbiidae, Physidae, Ancylidae y Sphaeriidae, y gran parte de los Hydrobiidae, son muy pobres en representantes fósiles, y son taxa de distribución mundial muy antigua, no conociéndoce exactamente sus centros de dispersión originales.

En general, el resultado de nuestro estudio confirma, en gran parte, las hipótesis anuncidas por Pilsbry en la primera década de este siglo, y en crédito a ese autor puede agregarse que, no teniendo suficientes fósiles conocidos en que basarse, las conclusiones a que Pilsbry llegó por su buen conocimiento de las faunas vivientes, aún se mantienen, con excepción de pocas modificaciones.

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